PIPID FROGS FROM THE EARLY CRETACEOUS OF ISRAEL AND PIPID EVOLUTION

EVIATAR NEVO[1]

CONTENTS

Abstract 255
Introduction 255
Acknowledgments 256
Geology 257
Paleoecology 260
Materials and Methods 261
Systematic Descriptions 263
  Thoraciliacus rostriceps, n.g., n.sp. 265
  Cordicephalus gracilis, n.g., n.sp. 269
  Cordicephalus longicostatus, n.sp. 272
  Osteological summary 274
Variation 276
Discussion 282
  Relationships and Evolutionary Interpretation of Ramon Frogs 282
  The Systematic Position of *Cordicephalus* and *Thoraciliacus* and Remarks on Pipoid Classification 295
  Pipoid Evolution 299
Summary and Conclusions 304
References Cited 304

ABSTRACT

The discovery of a horizon rich in frogs in the lower early Cretaceous of Makhtesh Ramon, Israel, is recorded, and the geology, age, paleoecology, fauna, flora, and climate are discussed. Articulated frog skeletons comprise most of the fauna. They are described as two new pipid genera including three species: *Thoraciliacus rostriceps*, 800 specimens; *Cordicephalus gracilis*, 49 specimens; and *Cordicephalus longicostatus*, 14 specimens. All species are aquatic, variable, and represent a melange of 21 primitive and 16 specialized characters. In all, the pelvis, skull, and pectoral girdle are highly variable, the limbs less so. The skull, pelvis, and limbs are essentially specialized, the column and pectoral girdle primitive. *Thoraciliacus* is more aquatic, variable, and specialized than *Cordicephalus*, yet both are the most primitive and earliest sure pipids known. The thoraciliacid line is related to South American and African Cretaceous pipoids; it flourished in the Cretaceous, and became extinct in the Tertiary, while *Cordicephalus* is on the ancestral line of Tertiary xenopids. Reevaluation of pipid classification does not support a separate family for Cretaceous pipoids which may be referred to Recent Pipidae.

Ramon pipids suggest that pipids pursue a progressive primary aquatic adaptation, this operating as the main evolutionary selective factor since their probable Triassic origin from proanurans. Pipids have probably never been taxonomically prolific, but their record suggests a rapid basic diversification, extinctions, and slower later evolution. Evolutionary trends since early Cretaceous times involve a series of structural changes, explicable as progressive improvements in aquatic adaptations. Pipids had an almost worldwide distribution in Cretaceous and probably Upper Jurassic times, but their center of origin is still obscure.

INTRODUCTION

The fossil record of Anura is traceable back to the early Jurassic, yet our ideas of the evolution of frogs are still mainly derived from studies of Recent forms (Griffiths, 1963; Tihen, 1965). This fact stems from a general conviction that the fossil record is incomplete, that fossil frogs are scarce, and that those known are essentially modern in their osteology. The first of these views is still justified so far as the early, presumably Triassic, transition period from proanurans to anurans is concerned. The gap between the earliest known true frog, *Vieraella herbstii* (Reig, 1961) from the Lower Jurassic of Argentina, and the possible ancestor, *Triadobatrachus massinoti* (Piveteau, 1937) from the Lower Triassic of Madagascar, is still neither documented by fossils nor in any way illuminated by Recent frogs. This gap can only be expected to be bridged, at least in part, when future finds from continental Triassic deposits unveil the transitional forms which linked proanurans to anurans.

---

[1] Department of Zoology, The Hebrew University, Jerusalem, Israel.

However, recently discovered fossil evidence (Nevo, 1956, 1964b; Reig, 1957, 1959, 1961; Hecht, 1963; Casamiquela, 1961a, b, 1965; Špinar, 1963; Estes, 1964) has partly elucidated patterns of Jurassic and Cretaceous frog evolution. Our knowledge of early anuran history has greatly increased during the last few years and has been partly reviewed by Hecht (1963). Significantly, the recent finds of large collections, involving complete frog skeletons, consist mainly of aquatic forms from the Cretaceous of South America, South Africa, Asia, and the Tertiary of Europe. Most other fossil frogs are fragmentary, apparently the result of the preservation characteristic of terrestrial habitats.

The available record of fossil frogs confirms in part earlier evolutionary hypotheses based on Recent forms, negates others, and contributes to the postulation of new ideas. It suggests the Triassic as the transition period from proanurans to anurans. It indicates the existence of three (and implies the presence of a fourth) independent anuran offshoots in Jurassic times consisting of the families Ascaphidae, Discoglossidae, Pipidae, and possibly some more advanced frog families. The record suggests two major adaptive radiations: first, an aquatic radiation during the Triassic and Jurassic; second, a terrestrial one during Jurassic and Cretaceous times continuing into the Tertiary. Finally, the record suggests possibilities for the objective evaluation of variation, evolutionary trends, phylogenetic and paleogeographic patterns.

The present paper is a first part of population studies on a collection of early Cretaceous frogs from Makhtesh Ramon, Israel (Nevo, 1964b). The amphibian zone, encountered accidentally during geological studies in Makhtesh Ramon in 1954 (Nevo, 1956), has already yielded 863 postmetamorphic, mostly articulated, frogs, one tadpole, and recently 14 urodeles (Nevo, 1964a). The frog collection consists of two genera comprising three species of aquatic pipid frogs. This paper describes the geology, environment and age of the amphibian bed, and the morphology and systematic relationships of the new forms. Pipoid classification is reviewed, suggesting that all hitherto known Cretaceous pipoids should be allocated to the Recent family Pipidae. Finally, the phylogeny, evolutionary trends and paleogeography of pipoids as suggested by this study are presented.

It is my conviction, explicitly reflected in the population studies, that the available fossil record of frogs, particularly of aquatic forms, is more complete than has been realized and that it permits a more objective approach to evolutionary studies. Furthermore, as I will later report, the Ramon collection proved suitable for demographic analysis both intra- and interspecifically, providing insight into population structure and dynamics of Cretaceous pipid frogs.

ACKNOWLEDGMENTS

This paper is part of a thesis submitted to the Department of Zoology of The Hebrew University of Jerusalem as partial fulfillment of the requirements for degree of Doctor of Philosophy, March 1964. The

manuscript was revised and completed during tenure of a Committee on Evolutionary Biology Traineeship at the Museum of Comparative Zoology.

This study was carried out under the guidance of Professor G. Haas, to whom I am especially grateful for his encouragement and great interest. I am deeply indebted to my colleagues who participated in the field trips. I have profited much by correspondence and/or discussions with Drs. C. G. S. de Villiers, N. F. Paterson in South Africa; F. Stadmüller, in Germany; O. A. Reig, R. Casamiquela in Argentina; Z. Špinar, Czechoslovakia; A. Parnes, Z. Reis, I. Zak, A. Arad, E. Mazor, J. Lorch, M. Glikson, G. Mishnaevski, in Israel; T. H. Eaton, R. Estes, E. C. Olson, E. E. Williams in the U.S.A.; R. Oldham in Nigeria. Each contributed many constructive suggestions and criticism of the MS in whole or in part. I am particularly indebted to Dr. I. Griffiths in England for the stimulating discussions we held on various aspects of this study.

Many thanks are due to Drs. Carl Gans, R. Oldham, E. E. Williams, and Mrs. J. Lundelius for their tedious editorial contributions. Special thanks are due Mr. Eli Minkoff who gave much of his time in discussion and statistical analysis. I am grateful to the following persons for either providing or exchanging material: Drs. J. L. Perret, Cameroons; G. Reverberi, Palermo; C. A. du Toit, Stellenbosch; O. A. Reig, Buenos Aires; Ch. Stadie, Kiel; A. G. C. Grandison, British Museum (Natural History), London; R. F. Inger, Field Museum, Chicago; C. M. Bogert, R. G. Zweifel, American Museum of Natural History, New York; M. Wahrburg, Adelaide. Some of the photographs were prepared in Dr. Estes' laboratory; I am thankful to him for his courtesy and time expended.

GEOLOGY

Figs. 1, 2, 3; Pls. 1, 2

General. Makhtesh Ramon, the central breached part of the Ramon anticlinorium in the central Negev, Israel, is an erosion cirque 30 km in length with a maximum width of 8 km (Fig. 1). Its exposed rock sequence ranges in age from Middle Triassic to Cenomanian, totalling some 1200 m. The sequence consists of alternating marine and continental sediments. While the Triassic and Cenomanian strata are mainly of marine origin, the Jurassic and Lower Cretaceous beds are mostly terrestrial (Bentor and Vroman, 1951; Nevo, 1955; Shilo and Nevo, 1955; Israel Geological Society Symposium, 1963).

A generalized cross-section of the Lower Cretaceous in western Makhtesh Ramon is shown in Figure 2. The sequence, about 200 m thick, consists of "Nubian Sandstone," partly fluviatile and lacustrine, partly aeolian, with a thin marine intercalation. These Lower Cretaceous strata overlie Jurassic sediments with a pronounced angular unconformity, indicating tectonic activity at the end of the Jurassic. Extensive regression of the sea, followed by strong volcanic activity, ensued throughout the Middle East (Nevo, 1963). The resulting continental facies in the Ramon area provided the prerequisite environment for the eventual flourishing of the amphibians in early Cretaceous times.

Amphibian Hill. In Makhtesh Ramon, a regionally widespread alkaline basaltic sheet, 0–70 m thick, underlies the main Lower Cretaceous sandstones, forming a band along much of the surrounding cliffs of the cirque. The basalt sheet in western Ramon (Pl. 1 A, B) consists of two distinct flows. The amphibian zone is located between the two flows, extends over 0.25 km^2, and comprises few outcrops, the main one being 2.5 m thick and 20.0 m long (Figs. 1, 2, 3; Pl. 1 B, C). The rock consists of fine varve-like alternating dark and light laminations. The light laminations comprise silt and/or fine-grained angular quartzitic sandstone intermixed with clays, while the dark laminations are chiefly limonitic. Some laminations are continuous while others taper gradually or abruptly.

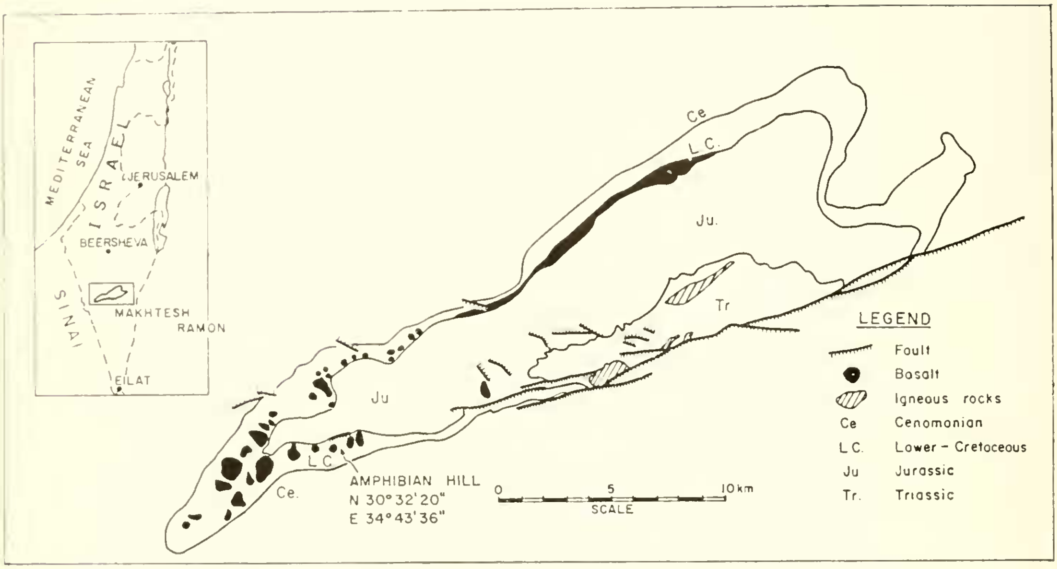


Figure 1. Location and geological map of Makhtesh Ramon.

Miniature cross bedding is visible in thin cross-sections (Pl. 1 D). The entire section contains several thousand laminations, a pair of dark and light laminae forming a "varve." The chemical analysis of the rock, in percentages, is as follows: SiO_2—54.04; Al_2O_3—16.21; TiO_2—2.71; Fe_2O_3—6.82; FeO—0.18; MnO—0.06; MgO—0.99; CaO—1.02; Na_2O—0.75; K_2O—10.00; P_2O_5—0.50; $-H_2O$—3.20; $+H_2O$—3.08; Organic material—0.08; Cl—traces; S, SO_3—0.00; CO_2—0.00; NO_3, B, F—0.00. The section contains volcanics, chiefly basalt, ash, tuffs, lapilli and bombs, indicating surrounding centers of eruption. Joints and minor faults abound in the sediment, which is diffused with limonitic red and black crusts reflecting diagenetic processes.

The numerous fossil frogs are unequally distributed throughout the deposit, yielding on the average some ten specimens per cubic meter. The number of frogs in the whole bed runs into the thousands, outnumbering all other remains. In all, 863 adult frogs and one tadpole have been collected, compared with 14 urodeles, two dinosaurian teeth, and plant remains. No other animal remains were found. While the amphibian burial assemblage was *in situ*, as indicated by the complete articulated skeletons, this was not true for all plant species, some of which were secondarily accumulated in the deposit.

Age of the amphibian zone (Fig. 2). The Lower Cretaceous sequence unconformably overlies strata of Jurassic age (Nevo, 1955), and underlies those of Cenomanian age (Bentor and Vroman, 1951); for a list of Jurassic and Cenomanian fossils refer to Figure 2. Abundant plant remains occur throughout the sequence (Pl. 2); some indicate a general Lower Cretaceous age, whereas others point definitely to a pre-Albian, probably Neocomian age. *Weichselia reticulata* Stokes and Webb occurs throughout most of the sequence (Shilo and Nevo, 1955), indicating a Lower Cretaceous age (Teixeira, 1948). Figure 2 lists the plant assemblage associated with the fossil frogs (described by Lorch, 1963). The species *Brachyphyllum obesum* Heer, *Cladophlebis* cf. *browniana* Dunker, *Cladophlebis* cf. *dunkeri*, and *Desmiophyllum zeillerianum* are common in the Wealden, indicating a pre-Albian, probably a Neocomian age (Teixeira, 1948). A second

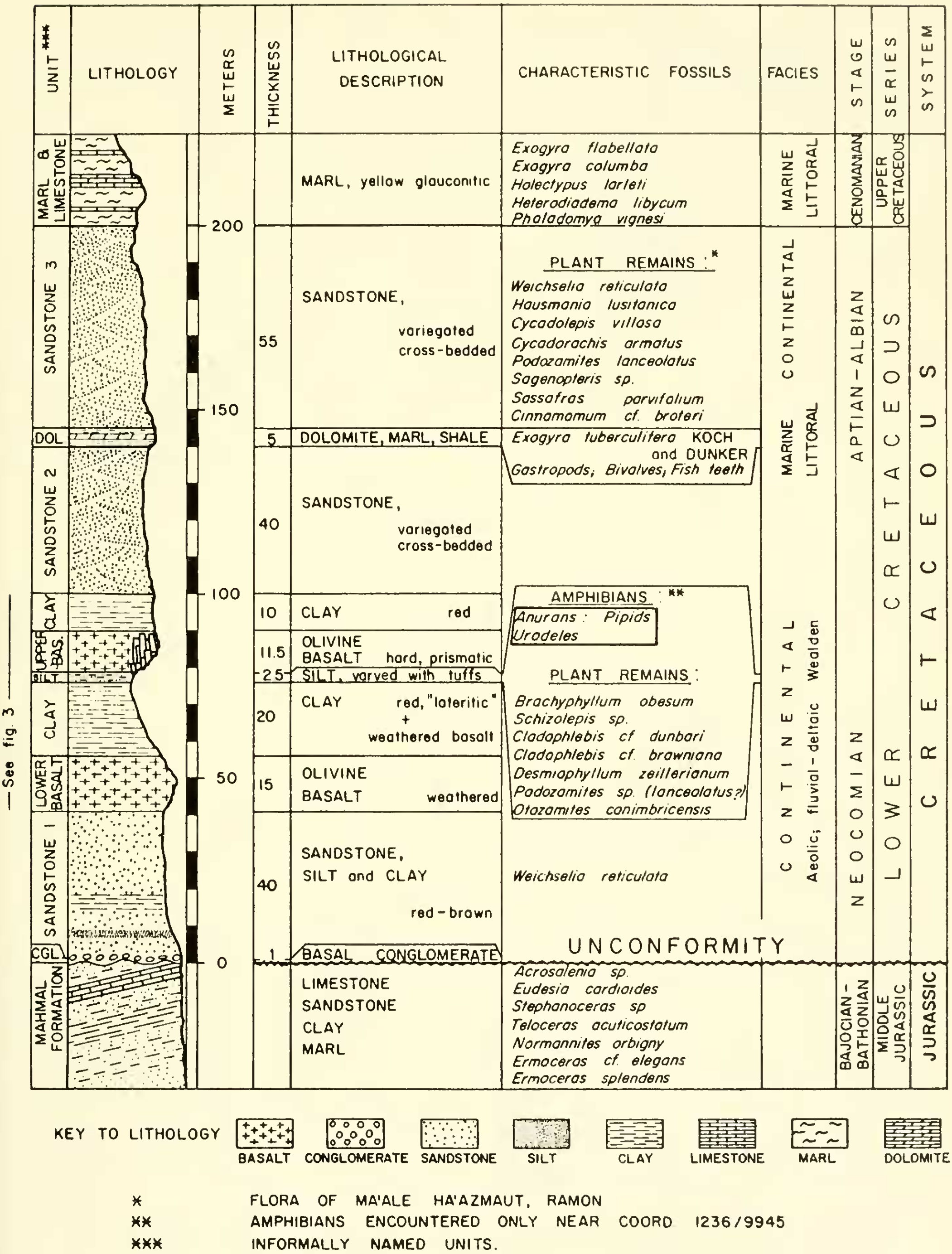


Figure 2. Generalized columnar secton, Lower Cretaceous western Makhtesh Ramon.

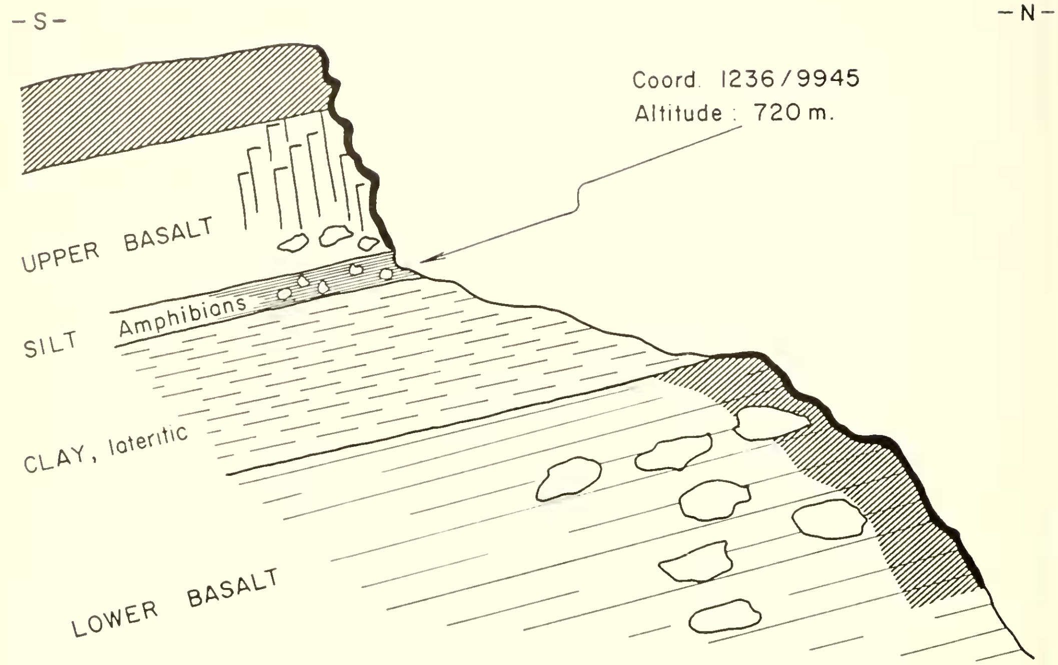


Figure 3. Geological cross-section (diagrammatic) through Amphibian Hill, Makhtesh Ramon (Longitude: E 34° 43′ 36″; Latitude: N 30° 32′ 20″).

plant assemblage, some 100 m above the former, in which *Weichselia reticulata* is associated with other filicales, gymnosperms, and dicotyledons, has been assigned an Albian age (Lorch, 1963). A further confirmation of the pre-Albian, probably Neocomian, age of the amphibian bed is furnished by the marine intercalation of the Lower Cretaceous, situated some 75 m above the amphibian zone (Fig. 2). The intercalation contains various ostracids, among them *Exogyra tuberculifera* Koch and Dunker, which ranges from the Valanginian to the Aptian, and is common in the Neocomian of Europe (Woods, 1912). Its occurrence indicates, at the most, an Aptian age for the marine intercalation (Mishnaevski, personal communication). In any event, since the amphibians occur near the bottom of the section, they belong to the lower part of the Lower Cretaceous.

No foraminifers or ostracods were found in the marine intercalation. The low concentrations as well as the unfavorable ratios in which Ru, Sr, K and Ar occur in the lower and upper basalts make these rocks extremely difficult for absolute age determinations (Mazor, personal communication).

PALEOECOLOGY

Climate. Several lines of evidence suggest a humid-warm climate in the Ramon area during Lower Cretaceous times. The first is the nature of the fossil frogs and the dinosaurian teeth. The frogs belong to the Pipidae, a purely aquatic frog family, comprising three genera and fifteen species, restricted today to tropical and subtropical regions of South America and Africa. The worldwide distribution of dinosaurian faunas in early Cretaceous times also implies tropical or subtropical climates (Colbert, 1964). The second is the formation of red lateritic clayey soil during the volcanic Lower Cretaceous basalt phase, particularly following the lower basalt flow and preceding the lake period. The third is the abundance of fluvio-deltaic sediments abounding with kaolinitic clays and rich in warm-type flora in early Cretaceous times. Finally, Lowenstam (1964), using Urey's oxygen isotope method, estimated average temperatures of 24° C for marine waters of Albian times at 30° N, as compared with 21° C at present.

Environment. The following habitat picture has been inferred from the geological, chemical, climatic, and biological data presented above. The evidence suggests that the frogs inhabited a small, shallow, freshwater lake having an outlet. A rich littoral vegetation bordered the lake: Bennettitales similar to *Otozamites*, conifers, including *Schizolepis, Brachyphyllum* and *Podozamites*, and ferns, including species of *Cladophlebis. Weichselia reticulata* predominated farther from the lake in the sandy habitats. The topography was low, composed of sandstone hills and scattered volcanoes. The lake lasted several thousand years at the most, and was apparently continuous throughout that time until dried up by the second or upper lava flow. The surrounding volcanoes erupted recurrently, pouring a part of their wastes into the lake, polluting the water and causing irregular mass mortalities among the frogs. Sedimentation in the lake was quiet, periodic, mostly in standing or very slowly flowing water.

The lake waters were warm, soft, possibly acidic, and abounded with decaying plants. The oxygen content was low with a reducing bottom. The latter resulted from a high H_2S content, typical of freshwater lakes in tropical regions and of volcanic environments. The lake bottom was presumably barren of all living organisms except anaerobic bacteria, thus providing ideal conditions for frog preservation, resulting in complete intact skeletons, undisturbed by any scavengers. The lake was thus oligotrophic and probably had a low productivity caused by the low content of nitrates, phosphates, and carbonates, high stagnation, poor aeration and not infrequent ash falls from the surrounding volcanoes. In all, the fauna was very poor in species, apparently reflecting the general unfavorable condition of the lake water. The food sources of the frogs and urodeles remain a riddle.

MATERIALS AND METHODS

Field work. This study is based on 863 postmetamorphic fossil frogs of which 344 were studied in detail. All the material was collected by the author and many colleagues during the period 1954–1962 from the same outcrop in western Makhtesh Ramon, Israel (Figs. 1, 2, 3; Pl. 1).

The collecting consisted of recovering slabs of rock, mainly by hammer and chisel. Only once were explosives used to get rid of the basaltic overburden. The original layering greatly facilitated the recovery of slabs that were later cleaved by light hammer strokes along the fine varves in order to reveal the frogs. These were easily detected by following the limonite-encrusted varves. Cleaving was done either in the field or in the laboratory. After cleaving, portions of the skeleton remained on both sides of the slabs as part and counterpart. The extreme fragility of both matrix and fossils required efficient packing and careful transporation from field to laboratory.

Preservation of fossils. Most of the material was preserved as complete skeletons, with only a few single bones or masses of disarticulated elements. The method of recovery of the material from the deposit and the extensive jointing within the sediment resulted in a high frequency of fractures. Preservation varies from excellent to poor. About 10 per cent of the specimens are mere imprints in the silt and therefore unworkable; the rest are preserved as either limonitic original bones or colored imprints. The skeletons were replaced, partially or entirely, by ferric oxides. The finer the sediment the better was the preservation. Preparation was hampered by the fragility

Table I. Comparative Recent and Fossil Material Studied

Family	Species	Provenance	No. of Specimens
RECENT			
Ascaphidae	*Ascaphus truei*	Washington (state), USA	3
"	*Leiopelma hochstetteri*	New Zealand	1
Pipidae	*Pipa pipa*	Brazil, British Guiana	3
"	*Hemipipa carvalhoi*	Brazil	1
"	*Hymenochirus boettgeri*	Cameroons	10
"	*Xenopus laevis*	Stellenbosch, South Africa	5 adults 5 larvae
"	*Xenopus tropicalis*	Niapu, Congo	3
"	*Xenopus gilli*	South Africa	3
"	*Xenopus mulleri*	Farjade, Congo	3
Discoglossidae	*Discoglossus pictus*	Sicily	10
"	*Discoglossus nigriventer*	Israel	1
"	*Bombina bombina*	Italy	2
"	*Bombina variegata*	Italy	10
"	*Alytes obstetricans*	Europe, locality unknown	2
"	*Alytes cisternasii*	Spain	1
Rhinophrynidae	*Rhinophrynus dorsalis*	Mexico	3
Pelobatidae	*Pelobates syriacus*	Haifa, Israel	3
"	*Pelobates fuscus*	Germany	2
"	*Scaphiopus holbrooki*	Texas, USA	2
"	*Scaphiopus couchi*	Texas, USA	2
"	*Scaphiopus hammondi*	Arizona, USA	2
"	*Megophrys hasselti*	Philippine Islands	2
Leptodactylidae	*Rhinoderma darwini*	Chile	1
"	*Leptodactylus ocellatus*	Brazil	2
"	*Leptodactylus bufonius*	Argentina	4
Bufonidae	*Bufo bufo*	Germany	2
"	*Bufo viridis*	Saar, Israel	15
"	*Bufo typhonius*	Venezuela	4
Pseudidae	*Eleutherodactylus nasutus*	Brazil	1
Hylidae	*Hyla arborea*	Saar, Israel	5
Ranidae	*Rana ridibunda*	Oranim, Israel	10
FOSSIL			
Pipidae	*Saltenia ibanezi*	Cretaceous, Argentina	5
	Hekatobatrachus grandipes	Miocene, Czechoslovakia	2

of the skeletons. During fossilization there was crushing and flattening of the skeletons, thus eliminating some structural details; consequently, the description is composite.

Laboratory work. The material was examined under binocular microscope while immersed in xylol to disclose features not observable in the dry specimens. Some 200 specimens in xylol were photographed on Kodak microfilm. Line drawings were made by tracing projected negatives.

The fossil material was compared with skeletons of living frogs, utilizing X-ray photographs (particularly for studying variation [Vose, 1958]), alizarine-red S transparencies (Williams, 1941), and dry skeletons (Sanders, 1953). Table 1 lists the skeletons of Recent species examined.

Statistics. Vernier caliper measurements were made to 0.1 mm on 248 fossil skeletons under the binocular dissecting microscope; 28 variates were recorded. No specimen was sufficiently complete to permit all 28 measurements. The data were analyzed using four IBM 7090 7094 computer programs for generating new variables, univariate statistics, scatter diagrams and histograms, and computing Mahalanobis distance among the three species. (The detailed biometric results and a study of variation will be reported in a separate paper.)

Location of material. The collection is deposited in the Department of Zoology, Hebrew University of Jerusalem (HUJZ). Of the 863 specimens in the collection, only 344 were numbered systematically. The prefix F runs before the number, whereas suffix a or b runs after it, designating part and counterpart whenever present; e.g. F 241 a and F 241 b.

SYSTEMATIC DESCRIPTIONS

Family PIPIDAE

THORACILIACUS gen. nov.

Type species. *Thoraciliacus rostriceps* sp. nov.

Diagnosis. A pipid closely related to *Eoxenopoides reuningi, Shelania pasquali*, and *Saltenia ibañezi* (see Table 8), but differing from these in having a free monocondylar sacro-urostylar articulation and one or more discrete postsacral vertebrae; in the absence of a suture between the frontoparietals; in the prominent rostrum; in the maxillae and premaxillae bearing teeth; in the sword-like parasphenoid; in the triangular transverse processes of presacrals 6–8; and in the articulation of tips of the ilia with the ribs.

Generic description. An anuran of pipid affinity. *Vertebral column*: Eight opisthocoelous, ectochordal presacral vertebrae; sacrum consisting of the 9th opisthocoelous vertebra with strongly expanded diapophyses; usually one postsacral vertebra; four pairs of free ribs attached to presacrals 2–5; diapophyses of presacrals 6–8 triangular and anteriorly directed; urostyle free from sacrum, with a single condyle. *Pectoral girdle*: Arciferous; clavicles large, strongly arched, meeting anteriorly, overlying the scapula posteriorly; coracoids strongly diverging from clavicles, straight shafts expanded at both ends much more mesially where they meet; scapula small, triangular, uncleft; suprascapula large, elongated, feebly ossified, supporting a large, strongly ossified V-shaped cleithrum; no sternum and episternum. *Skull*: Large, broader than long, quadrate region posteriorly situated; nasals large, forming a prominent anteriorly rounded rostrum; frontoparietals azygous, vase-shaped, large, strongly ossified; premaxillae with 10 teeth; maxillae with 35 teeth, tapering posteriorly without any contact with the quadrate [an incomplete maxillary arcade]; squamosals slender, small. No quadratojugals, palatines or mentomandibulars; vomers small, paired, anteriorly triradiate; pterygoids large with anteriorly thinning arcuate extensions; quadrate subquadrangular, well ossified; parasphenoid sword-like, its anterior tapering blade protruding in front of the maxillae, its posterior third wider, broadening into short lateral processes; sphenethmoid single, ossified, protruding anteriorly between nasals; otic capsules extensive, almost spherical; plectrum of columella outstanding; lower jaw comprises slender edentulous dentary, and prominent prearticular. *Pelvic girdle*: Large; ilia long, extending anteriorly beyond sacral diapophyses, their tips articulating with ribs 3 and/or 4; pubis strongly ossified; ischium long, ossified; no epipubis. *Forelimb*: Humerus straight, mostly smooth, with a small proximal ventral crest, proximally expanded, distally having a well-developed spherical capitate eminence; radioulna single, flat, expanded at both ends, with a prominent olecranon and a longitudinal intermedial groove; nine carpals; four subequal fingers with very long slender metacarpals and 2, 2, 3, 3 phalanges, the terminals of which are pointed; no prepollex. *Hindlimb*: Femur faintly S-shaped with a short femoral crest; tibiofibula single, slightly shorter than femur, with a longitudinal intermedial groove; tibiale-fibulare elongated, fused at both ends; five distal tarsals; no prehallux phalanges; five toes with long metatarsals and 2, 2, 3, 4, 3 phalanges, the terminals of which are

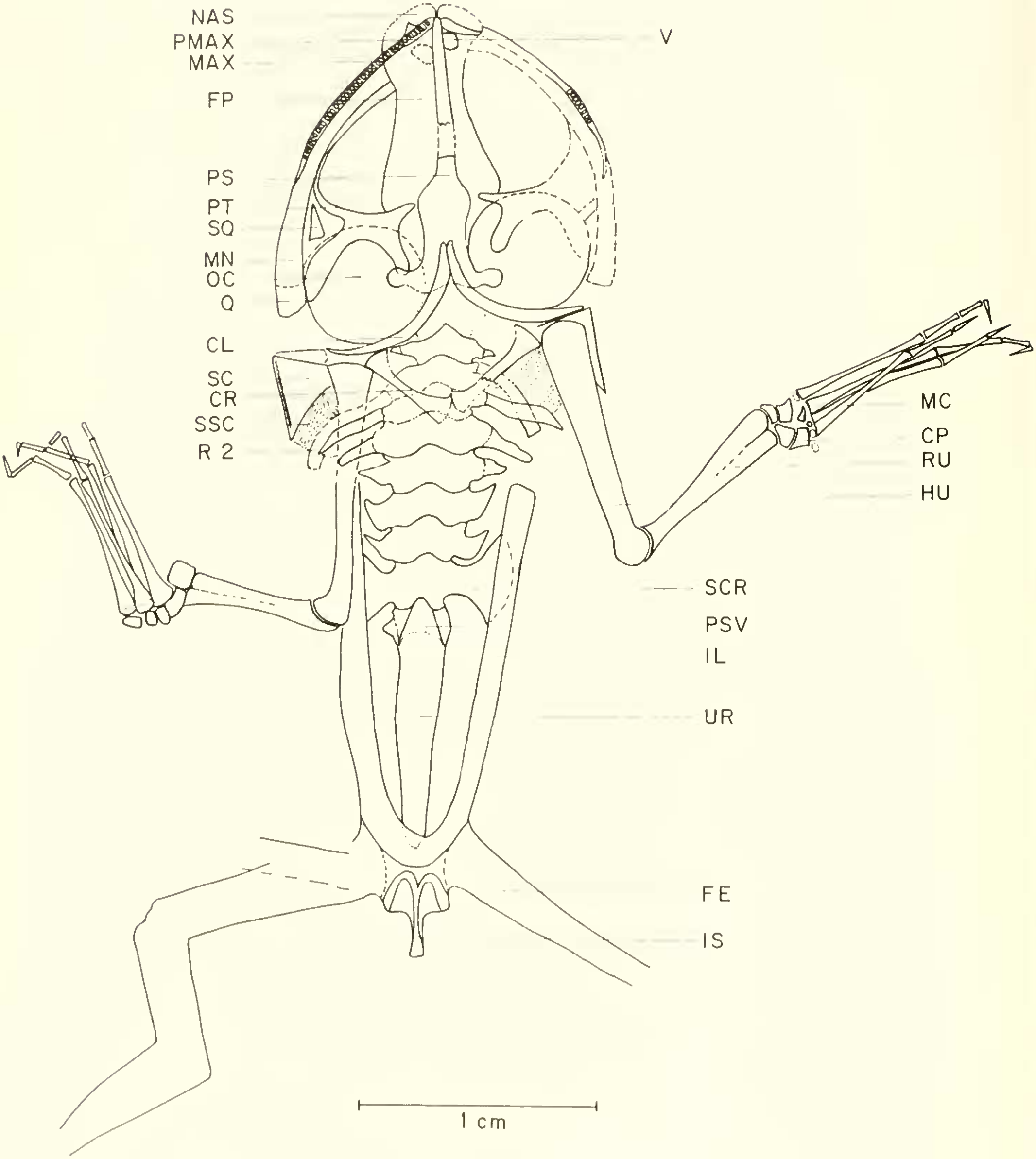


Figure 4. *Thoraciliacus rostriceps*, HUJZ, F 93, type specimen, ventral aspect. Abbreviatons: CL-clavicle; CP-carpal; CR-caracoid; FE-femur; FP-frontoparietals; HU-humerus; IL-ilum; IS-ischium; MAX-maxilla; MC-metacarpal; MN-mandible; NAS-nasal; OC-otic capsule; PMAX-premaxilla; PS-parasphenoid; PSV-postsacral vertebra; PT-pterygoid; Q-quadrate; R2-rib 2; RU radioulna; SC-scapula; SCR-sacrum; SQ-squamasal; SSC-suprascapula; UR-urostyle; V-vomer.

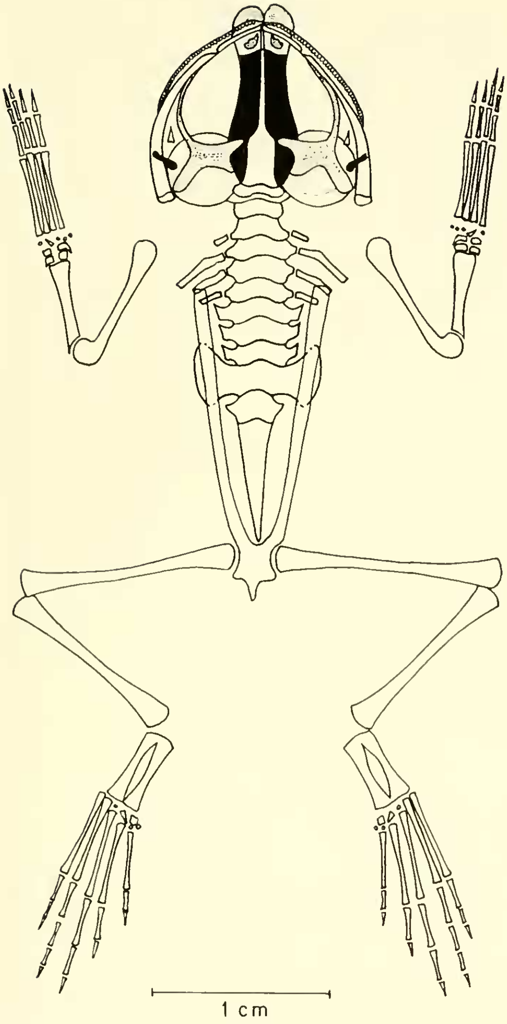


Figure 5. *Thoraciliacus rostriceps*, reconstruction.

pointed; all epiphyses of long bones in both fore- and hindlimb are well ossified.

Thoraciliacus rostriceps sp. nov.

Figs. 4, 5, 10–13; Pls. 3–6; Tables 2, 3

Holotype. Hebrew University, Jerusalem, Department of Zoology No. F 93, nearly complete skeleton lacking most of the hindlimbs (Pl. 3 A).

Hypodigm. Type and specimens F 1–148, 210–240, 247–250, 253.

Horizon and locality. Silt unit between lower and upper basalts, Lower Cretaceous (Fig. 2). Coordinates 1236/9945 (Israel Topographical Map); latitude: 30° 32′ 20″ N; longitude: 34° 43′ 36″ E; western Makhtesh Ramon, Israel; collected by Eviatar Nevo in 1954.

Specific diagnosis. Same as for genus; sole known species of the genus.

Description of the type material. A well preserved small frog represented by the original bones heavily impregnated by dark limonitic ferric oxides; distinctly flattened as a result of fossilization. Right hindlimb crushed proximally, and both hindlimbs lacking distally; in ventral aspect. Absent parts are described from F 41 a (Pl. 6 E).

General description. Skull (Fig. 10 C). The skull is large, wide and flat. It is somewhat broader than long, slightly longer than the eight presacral vertebrae. The maxillary arcade is incomplete. A prominent rounded rostrum projects beyond the mouth. The quadrate region is posteriorly situated. The nasals are large, broad and kidney-shaped, rounded anteriorly and forming the rostrum (Pl. 6 D); they meet anteromesially and diverge posteriorly to expose the central extension of the sphenethmoid; dorsally they have fanlike striations.

The frontoparietals form a broad azygous slab, strongly and totally ossified; they dominate the dorsal aspect of the skull and have a vaselike shape; anteriorly they contact the sphenethmoid; posteriorly they partly overlap the synotic region; the lateral portions are anteriorly concave, posteriorly convex, and exhibit slightly thickened supraorbital ridges. The premaxillae are overlain by the nasals and have a small triangular facial process; each premaxilla carries 10 teeth, mostly recognizable by their sockets. The maxillae are gently curved, tapering posteriorly to end in front of the posterior border of the orbit, or just at this level; since the quadratojugals are absent and no contact exists with the quadrate, a considerable gap obtains between the maxilla and quadrate, resulting in an incomplete maxillary arcade. A maxillary frontal process forks anteromesially, ending freely. Each maxilla carries 35 teeth evenly spaced throughout its entire length; mostly the teeth are recognizable through their sockets, but in F 63 conical little teeth are preserved.

The squamosals are small, slender, rodlike or triangular bones, apposing the otic capsules. The quadratojugals and palatines are absent. The vomers are small, paired, anteriorly triradiate, the median projection being the longest; they are only rarely preserved (F 36, 85, 93, 112, 293). The pterygoids are well developed, overlapping the anterolateral portions of the otic capsules. Their broad root is triradiate; the anteromesial arm is short, contacting the broader part of the parasphenoid; the posterolateral arm is the longest of the basal processes and contacts the quadrate; the broad root extends anterolaterally to meet the maxilla as a long, anteriorly thinning arcuate extension. The quadrate is subquadrangular, small, well ossified and only rarely visible (but can be seen in F 47, 52, 112, 120, 321). The parasphenoid is sword-like and prominent along the ventral aspect of the skull from the mid-otic capsules, posteriorly, to near the edge of the rostrum in front of the maxillary arcade; its anterior two-thirds consists of a narrow tapering rod, the "blade," while the posterior third is much wider and broadens into short lateral processes (Pls. 4 B, 6 C); the bone is rarely preserved complete (it is complete in F 20, 39, 93, 270, 309, 310), but is frequently represented just by its anterior acuminate portion. The sphenethmoid is single, well ossified, and fills the gap between the frontoparietals and nasals. Posteriorly it is emarginated; anteriorly it protrudes between the nasals.

The otic capsules are formed by the strongly ossified, very large, spherical prootics, dominating the posterior skull and situated mainly anterior to the quadrate; they are partly overlapped dorsomesially by the posterior portion of the frontoparietals, while ventromesially they are bordered by the exoccipitals which form the occipital condyles. The position of the semicircular canals shows clearly inside the capsules in several specimens (e.g., in F 60, 83, 84, 109, 128, 135, 138, 252). The plectrum of columella is preserved in 20 specimens. It is a small but well-ossified rod, 2.15 mm long and 0.4 mm wide, slightly arched, with a little swollen base abutting upon the fenestra ovalis proximally, ending freely distally.

The lower jaw consists of the dentary and prearticular only, the mentomandibulars being absent. The dentary is slender, edentulous, and articulates with the outer side of the prearticular, terminating close to the posterior limit of the maxilla. The prearticular is very large, strongly ossified, forming the principal element of the lower jaw; it has a prominent coronoid process in close apposition to the pterygoid, articulating post-otically with the quadrate.

Vertebral column (Fig. 11 C). There are usually eight presacral vertebrae; no fusions occur between successive vertebrae throughout the column. The presacrals are similar in shape. The vertebrae are flat and broader than long, with flat neural arches and short neural spines. The latter do not imbricate and, in several cases, the vertebral centra are exposed in dorsal aspect. The centra are opisthocoelous and ectochordal, consisting of an ossified cylinder enclosing a hollow tube reminiscent of a persistent notochord. (This is clearly shown by the optical section through a transparent vertebra immersed in xylol, which shows an hour-glass effect; see F 36 on Fig. 15 and F 40 on Pl. 4 B.) The atlas is usually free of diapophyses. Presacrals 2–5 possess horizontally directed short transverse processes, articulating with the corresponding ribs; the transverse processes of presacrals 6–8 are highly diagnostic, being triangular, sharply pointed, and anteriorly directed.

Four pairs of free ribs are confined to

the 2nd, 3rd, 4th, and 5th presacrals, hereafter referred to as ribs 1, 2, 3, 4, the first rib arising from the transverse processes of the second vertebra, etc. (Pl. 4 B). The first rib is the smallest, mostly directed posterolaterally. The second rib is generally the largest, usually arcuate, and posterolaterally directed. A few specimens show faintly expanded impressions on tips of second ribs, probably indicating a cartilaginous link between ribs 2 and 3. The third rib is also large but usually smaller than the second. It is bent posterolaterally, nearly parallel to the second rib. The fourth rib is smaller than the preceding two, usually exceeding in length only the first rib. It is mostly posterolaterally directed, but occasionally is horizontal or even pointed anterolaterally. Partial fusions of ribs to their corresponding transverse processes are not rare. This is particularly true for the first and fourth ribs. Apart from a few inconclusive cases, no uncinate processes were found.

The sacrum consists of the ninth opisthocoelous vertebra and has strongly expanded diapophyses. The urostyle is free from the sacrum, articulating with the latter by a single condyle. It tapers posteriorly, reaching, and sometimes overlying, the pubis. The urostyle has as a rule one proximal vertebra.

Pectoral girdle (Fig. 12 C; Pls. 5 C, 6 C, F). The pectoral girdle is inferred to be arciferal on the evidence of the strongly diverging coracoids and clavicles. The clavicles are very large, strongly arched, and strongly ossified; their anteriorly expanded ends meet midventrally, reaching the anterior portion of the otic capsules. The coracoids are posteriorly directed, strongly diverging from the anteriorly directed clavicles; they are well ossified, stout straight shafts, expanded strongly at both ends, but more so posteriorly, where they meet. The scapula is a small, triangular, strongly ossified bone, having a posterior distal spur and a diagonal distal border; the proximal margin is normally uncleft, lacking the notch separating the acromial from the glenoidal process (Pl. 6 A, C). The suprascapula is a weakly ossified large petaloid blade, posteriorly elongated and rounded; it reaches the level of the 4th presacral, overlying the second and third ribs. The cleithrum is a large, V-shaped, strongly ossified bone, investing the anterior and lateral margins of the suprascapula; it has two osseous prongs, the posterior being stouter and shorter than the anterior; it was preserved in 39 specimens. No traces of sternum, episternum, coracoidal cartilages, or epicoracoidal horns were found.

Pelvic girdle (Fig. 11 C; Pl. 6 A, E). The most remarkable feature of the pelvis is the anterior extension of the tips of the long ilia, which make contact with the third and/or fourth ribs, rarely ending freely. Consequently, the ilia articulate with two or three extensions of the column, thus tending to bind together vertebrae four through nine. A functional synsacrum is thus formed, but no fusion of vertebrae occurs. (In this genus the tips of the ilia thus make an iliocostal contact, in addition to the contact effected with the sacral diapophyses at the middle or anterior portions of the ilia—"medioiliac" contact; these two articulations contrast with the normal single anuran "acroiliac" articulation—tip of ilium forming the contact with the sacral diapophyses. Hereafter, the *Thoraciliacus* condition will be consistently distinguished as iliocostal or medioiliac articulation from the acroiliac or more usual anuran articulation.) The ilia are simple and smooth in most cases, but are variable in form and divergence; mostly they are straight rods, but some are slightly convex externally either near the acetabulum or throughout their length; others are asymmetric. The ilia are longer than the vertebral column plus the sacrum. The pubis is strongly ossified. An important feature of the pelvis is the relatively great posterior extent of the ischium in most specimens. No traces of epipubis were found.

Forelimb (Fig. 13 C). The humerus is

straight, expanded at both ends but distinctly more so towards the proximal end where it attains its maximal diameter, being capped by the well-ossified humeral cap; distally, it has a well-ossified, developed, spherical capitate eminence; the lateral epicondyle is very weakly developed, while the medial one is mildly so; the cubital ventral fossa is a small triangular pit; the shaft is distinctly smooth and crestless apart from the very short proximal ventral crest. No differences could be associated with sex. The radioulna is shorter than the humerus, single, flat and expanded at both ends, more so distally. Its dual origin is disclosed both by the intermedial groove extending over the distal two-thirds of its length, and by the presence of two distinct bones at the distal end; proximally, the olecranon process is prominent; no bony crests. There are nine carpals arranged in three rows; these are, following the nomenclature of Howes and Ridewood (1888): the radiale and ulnare in contact with the radioulna, two centrales in the second row, and five distal carpals in the third row. The radiale, ulnare, and centrales are big, subquadrangular, forming a characteristic tetrad; the inner centrale has a diagnostic posterior spur; all four are smooth dorsally but exhibit irregularities on their volar surface. The five distal carpals involve four small bones corresponding each to its respective metacarpal, and a small prepollex carpal discerned between the second carpal and inner centrale. The four distal carpals diminish in size in the following order: 4-2-5-3. Carpals 2, 3, 5, as well as the prepollex carpal, are small spheres, whereas carpal 4 has a diagnostic triangular shape. When the prepollex carpal is included, the total number of free carpals is nine. No phalangeal elements are associated with the prepollex carpal. No sex differences nor any fusions of carpals were discerned. Mostly the carpals are either missing or obscure; in only 28 out of 281 cases were they analyzable. This fate is shared also by the prepollex carpal because of its smallness and external position: it was eventually found in just four out of the above 28 specimens. (It is well preserved in F 297.) There are four elongated subequal fingers and 2, 2, 3, 3 phalanges, the terminals being pointed. The remarkable feature of the manus is the very long and slender metacarpals resulting in surprisingly long fingers.

Hindlimb (Fig. 13 C; Pls. 5 B, 6 E). The femur is strong, long, and shows a slight sigmoid curvature. It is expanded towards both ends where it has well-ossified epiphyses. The proximal femoral head is elliptical, fitting into the acetabulum of the same shape. Proximally, there rises a short, rather low femoral crest. The tibiofibula is even stronger, but slightly shorter, than the femur. It is approximately straight, being also expanded towards both ends, where it has well-ossified epiphyses. Its dual nature is disclosed throughout by the distinct intermedial groove. The tarsus consists of the characteristic tibiale-fibulare and five free distal tarsals. The tibiale and fibulare are elongated, broadening medially towards both ends where they meet, leaving a conspicuous interosseous space throughout their length. The tibiale is more slender than the fibulare. When seen entirely separated, as in F 36, they certainly suffered dislocation, suggesting a weak fusion. The distal tarsals are located between the inner three metatarsals and the tibiale, whereas the two outer metatarsals contact the fibulare leaving no space for any additional distal tarsals. The five distal tarsals involve a large centrale (= naviculare) attached to the tibiale, a prehallux tarsal in contact with the centrale, and a series of three smaller tarsals each corresponding to the three inner metatarsals. While both the first and third distals are small and round, the second is diagnostically large and triangular. There are five toes with strikingly elongated metatarsals, and 2, 2, 3, 4, 3 phalanges, the terminals being pointed. No phalanges are associated with the prehallux tarsal. The toes are unequal in length: The third is the largest and usually exceeds the fourth in length, but equals it in some cases; the second equals the fifth, the first toe being the shortest.

CORDICEPHALUS gen. nov.

Type species. *Cordicephalus gracilis*, sp. nov.

Diagnosis. A small anuran of pipid affinity, similar in most basic characteristics to *Thoraciliacus rostriceps*, from which it differs primarily in skull and pelvis (Figs. 10, 11, 13 and Tables 6, 7). The following are the features characterizing *Cordicephalus* as contrasted with *Thoraciliacus*: general slenderness of the entire skeleton; articulation of pelvic girdle acroiliac, with the tips of ilia articulating with sacral diapophyses; ilia diverging to form a triangle; ischium medium in length; skull heart-shaped (hence the generic name); no prominent rostrum; quadrate anteriorly placed; anterior extensions of pterygoid and mandible curved; otic capsules ellipsoidal or rectangular; third rib longer than second; transverse processes of presacrals 7 and 8 arcuate; one or two postsacral vertebrae; longer humerus and radioulna. See Table 4 for statistically significant differences between *Cordicephalus* and *Thoraciliacus*.

Cordicephalus gracilis sp. nov.

Figs. 6, 7, 10–13; Pls. 7–9; Tables 2, 3

Holotype. Hebrew University, Jerusalem, Department of Zoology No. F 165, nearly complete skeleton, lacking some portions of the pectoral girdle.

Hypodigm. Type and specimens F 149, 151, 153–155, 157–166, 168–170, 172, 174–187, 190–191, 197–209.

Horizon and locality. Same as for *Thoraciliacus rostriceps.*

Specific diagnosis. A very small *Cordicephalus*; no rostrum; nasals in form of crescentic bars; wide rear portion of parasphenoid having lateral processes both anteriorly and posteriorly; sphenethmoid with long triangular anterior prolongation; otic capsules ellipsoidal; ribs medium to long; sacral diapophyses broadening gradually distally; mostly two postsacrals; ilia diverge by about 45°; scapula uncleft; suprascapula triangular.

Description of type material. A well-preserved small and slender frog represented by original bones, heavily impregnated by dark limonitic ferric oxides. Slightly flattened due to fossilization.

Skull (Fig. 10 B). The skull is slightly broader than long, with a heart-like shape. The maxillary arcade is incomplete, and there is no rostrum. The quadrate region is anteriorly situated. The nasals overlie the premaxillae, in line with the maxillary arch, and form a rounded anterior contour. They are well-developed, elongated, crescentic bars, meeting mesially above the anterior arrow-like extension of the sphenethmoid and fitting closely into the anterior concave margins of the latter. The frontoparietals form an azygous, vaselike, strongly and totally ossified slab, approximating in shape, relations and contacts that of *T. rostriceps.* No median suture or pineal foramen were found in ten specimens examined for these features. The premaxillae and maxillae follow closely the *Thoraciliacus* pattern. Both bones are dentigerous but have smaller numbers of teeth than in the latter genus; about 25 in the maxilla and 8 in the premaxilla. The maxillary arcade is incomplete due to the absence of quadratojugals. The squamosals are small, slender splints, rarely preserved. There are no quadratojugals and no palatines. The vomers are apparently disclosed in only two cases (F 168, 176), each being triangular, forming with its partner a rhomboid structure near the anterior tip of the parasphenoid. The pterygoids are well developed, characterized by their curved anterior extension. The quadrate is a subquadrangular, well-ossified bone. The parasphenoid is sword-like, as in *Thoraciliacus*, differing from the latter in having horn-like projections at the base of the blade. In most cases only the blade is preserved. The sphenethmoid is single, well ossified; its

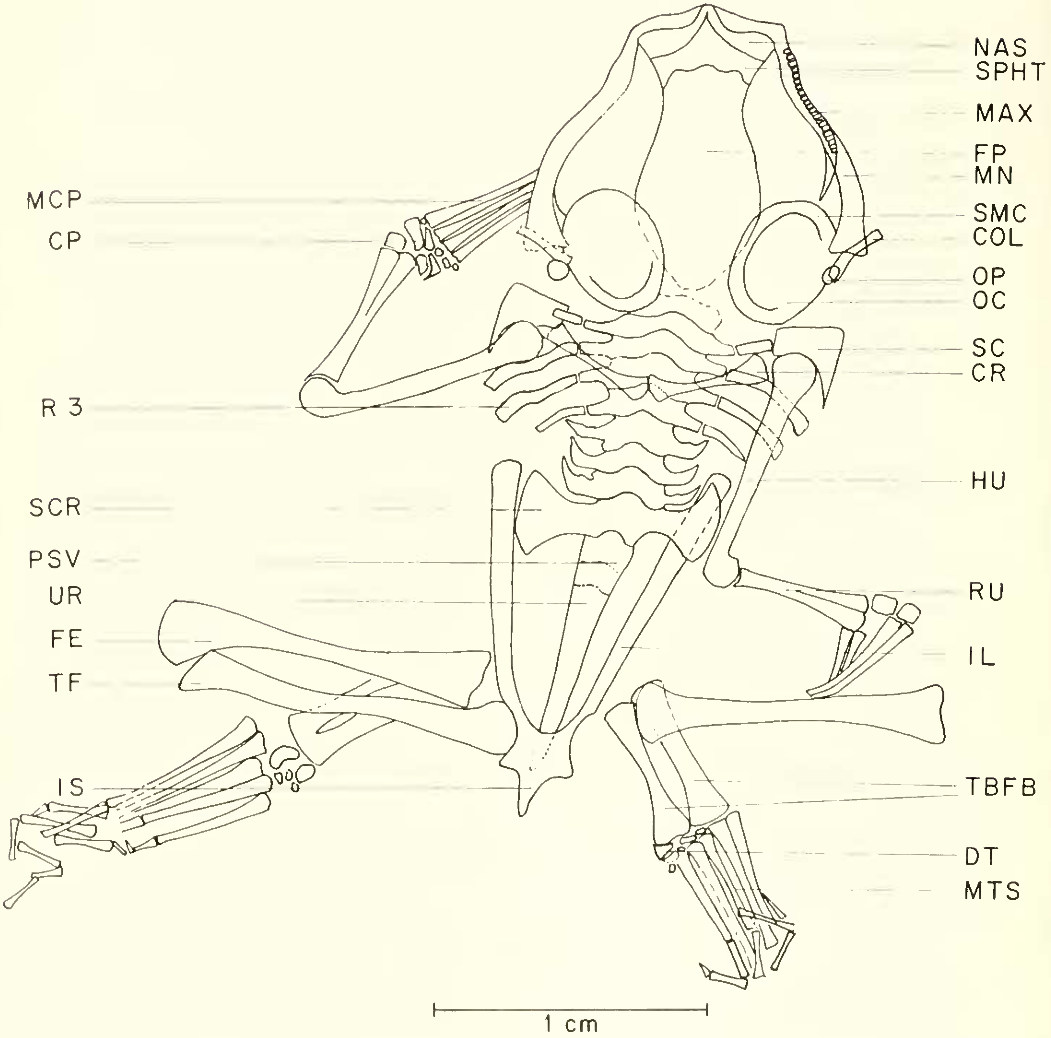


Figure 6. *Cardicephalus gracilis*, HUJZ, F 165, type specimen, dorsal aspect. Abbrevations: COL-columella; CP-carpal; CR-coracoid; DT-distal tarsal; FE-femur; FP-frontoparietals; HU humerus; IL-ilium; IS-ischium; MAX-maxilla; MCP-metacarpal; MN-mandible; MTS-metatarsal; NAS-nasal; OC-otic capsule; OP-operculum; PSV-postsacral vertebra; R3-rib 3; RU-radiaulna; SC-scapula; SCR-sacrum; SMC-semicircular canal; SPHT-sphenethmoid; TF-tibiofibula; TBFB-tibiale-fibulare; UR urostyle.

head projects distinctly to the front, much more than in *Thoraciliacus*. The otic capsules resemble those of *Thoraciliacus* in being extensive and intensely ossified, but differ in being obliquely ellipsoidal. The longitudinal axes of the two capsules form a right angle. Within the capsules the position of the semicircular canals shows clearly. The most remarkable feature associated with the capsules is the plectrum of the columella, seen in 8 specimens. It closely resembles the columella of *Thoraciliacus*, both in shape and size, but differs in its association with a small spherical ossified operculum, posterior to and abutting upon the fenestra ovalis (Pl. 9 D). It is

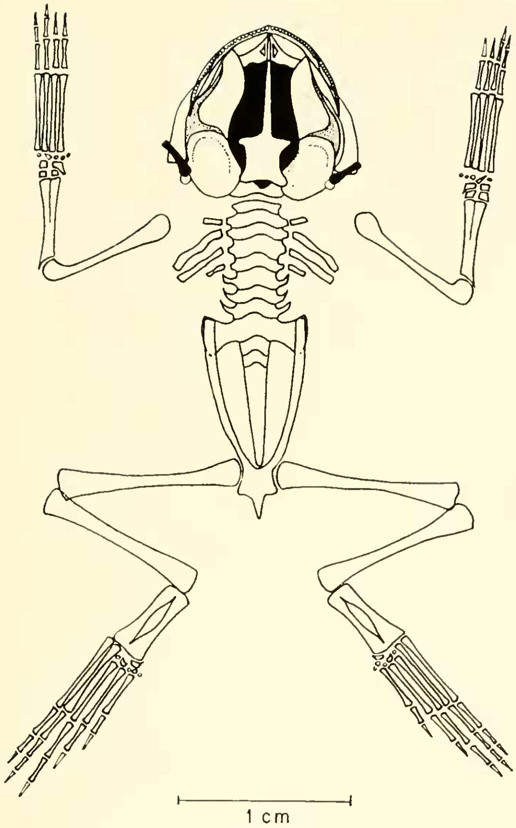


Figure 7. *Cordicephalus gracilis*, reconstruction.

probable that the swollen base of the plectrum represents the internal part of the columella, which was possibly ossified. The plectrum is 2.1 mm long and 0.3 mm wide. The lower jaw is arcuate, giving the skull, together with the anterior curved prolongation of the pterygoid, its heart-shaped form. It articulates pre-otically with the quadrate, thus differing from the post-otic condition of *Thoraciliacus.*

Vertebral column (Fig. 11 B). There are eight presacral vertebrae displaying no fusion. All are similar in shape, flat, broader than long. The neural arches are low; the neural spines short, non-imbricating, occasionally exposing the centra. The centrum is invariably opisthocoelous. The atlas is free of appendages. Presacrals two through five have relatively short transverse processes; those of presacral six resemble a more delicate version of the corresponding processes of *Thoraciliacus.* The transverse processes of presacrals seven and eight are highly diagnostic, differing basically from those of *Thoraciliacus*; they are arcuate as contrasted with the triangular ones of the latter, and anteriorly directed. Four pairs of slender ribs are confined to the second, third, fourth, and fifth presacrals, hereafter referred to as ribs 1, 2, 3, 4, the first arising from the transverse processes of the second presacral, etc. (Pls. 8 B, 9 G). The first rib is the smallest, directed anterolaterally. The third rib is the longest, followed in length by the second and fourth ribs, differing in this respect from *Thoraciliacus*, the second rib of which is the longest. The second through fourth ribs are posterolaterally directed, none ever having any contact with the tips of the ilia.

The sacrum consists of the ninth opisthocoelous vertebra, which has expanded diapophyses. The urostyle is free from the sacrum, articulating with the latter by a single condyle. It has in most cases a swollen base, tapering chiefly in its posterior two-thirds. Careful analysis, in xylol, disclosed in its proximal portion, otherwise obscure centra mostly lacking diapophyses; two postsacrals predominate.

Pectoral girdle (Fig. 12 B; Pl. 9 A, B). The pectoral girdle is arciferal, a delicate replica of the *Thoraciliacus* girdle and exhibiting only a few small differences from the latter. The clavicles are strongly arched and markedly diverge from the posteromesially directed coracoids. The latter are well ossified, stout, straight shafts, strongly and equally expanded at both ends, as contrasted with the more expanded mesial ends in *Thoraciliacus.* The two coracoids meet mesially. The scapula is small, roughly triangular, uncleft and intensely ossified. It resembles, but is wider than, the scapula of *Thoraciliacus.* The suprascapula is faintly ossified, triangular in shape; it supports a V-shaped cleithrum, having two well-ossified prongs, the posterior being stouter and shorter than the anterior (Pl. 9 B). No traces of sternum, episternum, or coracoidal cartilages were found.

Pelvic girdle (Fig. 11 B; Pl. 9 E). The pelvis forms a distinct triangle whose head angle is roughly 45°. The pelvic articulation being acroiliac, there is no functional synsacrum. (This is the fundamental difference between *Cordicephalus* and *Thoraciliacus.*) The tips of the ilia articulate with the sacral diapophyses only, having, in most cases, no projection anterior to the latter. In the few cases found of forward projection, the anterior slope of the ilia was apparently either natural, due to forward sliding of the ilia during movement (see p. 276), or an artificial shift caused by fossilization. The pubis is strongly ossified, and the ischium forms a medium-sized rear extension.

Limbs (Fig. 13 B; Pls. 7 A, B, 8 A). *Cordicephalus* does not differ essentially in its limbs from *Thoraciliacus* apart from slight differences in shape of particular bones and its generally more slender build.

Forelimb. The humerus is straight, smooth, and round in cross-section; distally, it has a well-ossified, developed, spherical capitate eminence (Pl. 9 B). The radioulna is single, flat, expanded at both ends, grooved throughout, and has a prominent olecranon. There are nine carpals arranged in three rows (Pl. 9 H). The two proximal rows comprise four big elements: radiale, ulnare, and two centrales. The inner centrale is diagnostically triangular, projecting distinctly to the rear. The five distal carpals involve four bones corresponding to each of the fingers, and one prepollex carpal. Again as in *Thoraciliacus*, the fourth distal carpal is the largest, diagnostically triangular, while the rest are essentially small spheres. There are four subequal fingers involving four very long and slender metacarpals, and 2, 2, 3, 3 phalanges, the terminals being pointed.

Hindlimb. The femur is slightly sigmoid in shape, expanded towards both ends. The tibiofibula is slightly shorter than the femur and is grooved throughout. The tibiale-fibulare are elongated, fused at both ends, leaving a conspicuous interosseous space throughout. The five distal tarsals involve a large centrale, the tarsal of a prehallux, and three smaller bones corresponding to the three inner metatarsals, the second being the largest. There are five toes with remarkably long and slender metatarsals, and 2, 2, 3, 4, 3 phalanges, the terminals being pointed. A rudimentary prehallux consists of only one small metatarsal.

Cordicephalus longicostatus sp. nov.

Figs. 8, 9, 10–13; Pls. 10, 11; Tables 2, 3

Holotype. Hebrew University, Jerusalem, Department of Zoology, No. F 171, crushed skeleton including parts of skull, column, girdles and limbs.

Hypodigm. Type and specimens F 150, 152, 156, 171, 173, 188, 189, 192–196, 251, 252.

Horizon and locality. Same as for *Thoraciliacus rostriceps.*

Specific diagnosis. Very similar to *Cordicephalus gracilis* from which it differs in its larger size and details of skull. See Table 5 for statistically significant differences between the two species. *C. longicostatus* is further diagnosed, as against *C. gracilis*, by having: a slight rostrum; large, subquadrangular nasals; slender frontoparietals; parasphenoid hornless at base of blade; sphenethmoid devoid of prominent anterior projection; otic capsules subquadrangular; long ribs; small cleft scapulae; suprascapulae posteriorly rounded; ilia divergent only to about 30°.

Description of type material. Badly preserved, crushed, small frog, represented by original bones impregnated by brown limonitic ferric oxides.

Skull (Fig. 10 A). The skull is similar to that of *C. gracilis*, from which it differs in the following characters: the subquadrangular nasals form a small triangular ros-

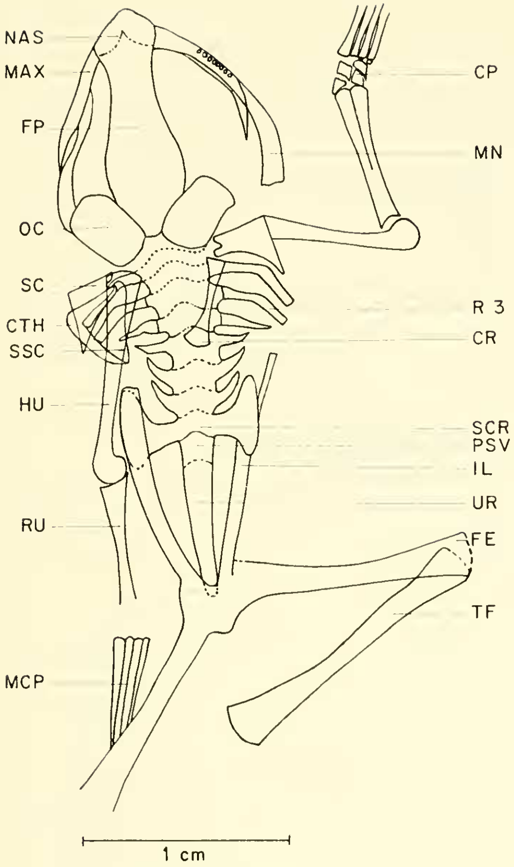


Figure 8. *Cardicephalus longicastatus*, HUJZ, F 171, type specimen. Abbreviations: CP-carpal; CR-coracoid; CTH-cleithrum; FE-femur; FP-frontoparietals; HU-humerus; IL-ilium; MAX-maxilla; MCP-metacarpal; MN-mandible; NAS-nasal; OC-otic capsule; PSV-postsacral vertebra; R3-rib 3; RU-radioulna; SC-scapula; SCR-sacrum; SSC-suprascapula; TF-tibiofibula; UR-urostyle.

trum. The anterior margin of the sphenethmoid is shallow, less prominent, and the frontoparietals are vase-shaped and more slender than in *C. gracilis*. No describable remains were preserved of the pterygoid, quadrate, or vomer. The palatines and quadratojugals are absent. The parasphenoid apparently lacks the processes on base of blade and hilt. The otic capsules are subquadrangular; their axes form an acute angle. In F 188 there is a bent plectrum of columella, 2.3 mm long and 0.3 mm wide, having a swollen base (Pl. 11 B, E).

Vertebral column (Fig. 11 A). There are eight opisthocoelous presacral vertebrae. The atlas has no appendages. The transverse processes of presacrals six through eight resemble, but are slightly larger than, those of *C. gracilis*. The four pairs of ribs are a larger replica of the latter (Pl. 11 A, D). The sacrum consists of the ninth opisthocoelous vertebra, having strongly expanded diapophyses; the latter are connected to the centrum through a narrow bridge of bone broadening abruptly distally (Pl. 11 F). The urostyle is free from the sacrum, articulating with the latter by a single condyle. It may contain one to two postsacrals or lack them entirely.

Pectoral girdle (Fig. 12 A). The girdle is arciferal. The clavicles are strongly arched. The coracoids diverge strongly from the clavicles, being well-ossified, stout, straight shafts expanded at both ends but more so mesially. The scapula is small, roughly triangular, and cleft in all three analyzable specimens (F 171, Pl. 10; F 188, Pl. 11). The suprascapula is faintly ossified, having a rounded posterior margin rather than a triangular one as in *C. gracilis*. The suprascapula supports a well ossified V-shaped cleithrum. No traces of episternum, sternum, or coracoidal cartilages were found.

Pelvic girdle (Fig. 11 A). The pelvic articulation is acroiliac, the tips of the ilia articulating with the sacrum. The pelvis forms an elongated triangle whose head angle is roughly 30°. In both features of the pelvis it is distinguishable from *C. gracilis*, whose pelvis is shorter, having a head angle of roughly 45°. The pubis and ischium are strongly ossified. No traces of epipubis were found.

Limbs (Fig. 13 A). No essential meristic characters distinguish the limbs from those of *C. gracilis*, but differences do occur in shape and size. The humerus is a straight, very long, smooth shaft, expanding only near its ends, being subequal in diameter

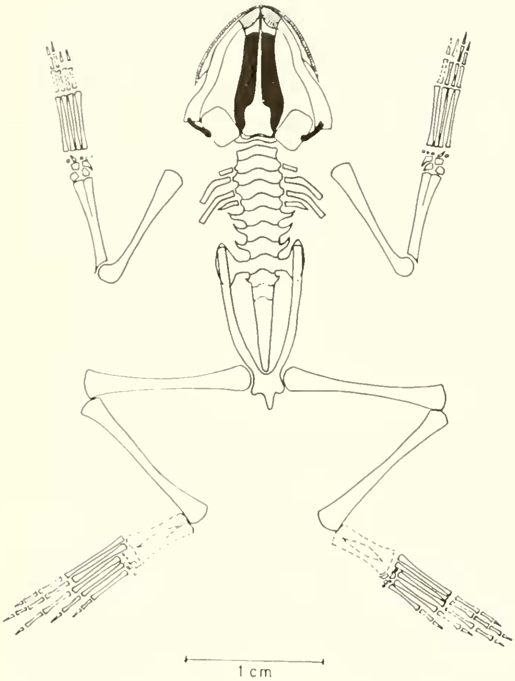


Figure 9. *Cordicephalus longicostatus*, reconstruction.

throughout its length. The capitate eminence is well developed. The radioulna is relatively long, having a well-developed olecranon process (Pl. 11 C). There are nine carpals and four subequal fingers involving very long metacarpals, as in *C. gracilis*. In no specimens were the phalanges entirely preserved; the phalangeal formula is thus indeterminable. The terminal phalanges are pointed. The femur is faintly sigmoid in shape, greatly expanded at both ends, being slightly larger than the tibiofibula; the latter is grooved throughout. The tibiale and fibulare are relatively long. The five metatarsals are very long; the terminal phalanges are pointed.

OSTEOLOGICAL SUMMARY

The following list summarizes for each skeletal system the characters common to all three species, and also the skull, pelvis, and tarsal features distinguishing *Cordicephalus* from *Thoraciliacus*. (Shape differences between the two genera are not repeated. See Tables 6 and 7 for qualitative differences in skull and pelvis, Tables 4 and 5 for quantitative differences between *Cordicephalus* and *Thoraciliacus*.)

SKULL (Fig. 10)

1) Skull well ossified, broader than long.
2) Frontoparietals large, vase-shaped, azygous.
3) Premaxillae and maxillae dentigerous.
4) Maxillary arcade incomplete.
5) Otic capsules extensive.
6) Plectrum of columella well ossified and developed, slightly curved rod.
7) Pterygoids extensive, with a long anterior extension.
8) Parasphenoid sword-like, having only short basal processes.
9) Sphenethmoid single, pointed anteriorly.
10) Vomers paired and edentulous.
11) Quadrate subquadrangular and well ossified.
12) Nasals well developed, medium to broad in shape, forming a *prominent* rostrum only in *Thoraciliacus*.
13) Squamosals reduced.
14) Quadratojugals, palatines and mentomandibulars absent.
15) Mandible edentulous, consisting of a slender dentary and a stronger prearticular.
16) Supra-otic arm, annulus tympanicus and hyobranchial skeleton were not found.

VERTEBRAL COLUMN (Fig. 11)

17) Eight presacral vertebrae.
18) Sacrum consists of the ninth vertebra having greatly expanded diapophyses.
19) Postsacral vertebrae one in *Thoraciliacus*, or two in *Cordicephalus*.
20) Centrum ectochordal.
21) Vertebrae opisthocoelous.
22) Sacro-urostylar articulation free and

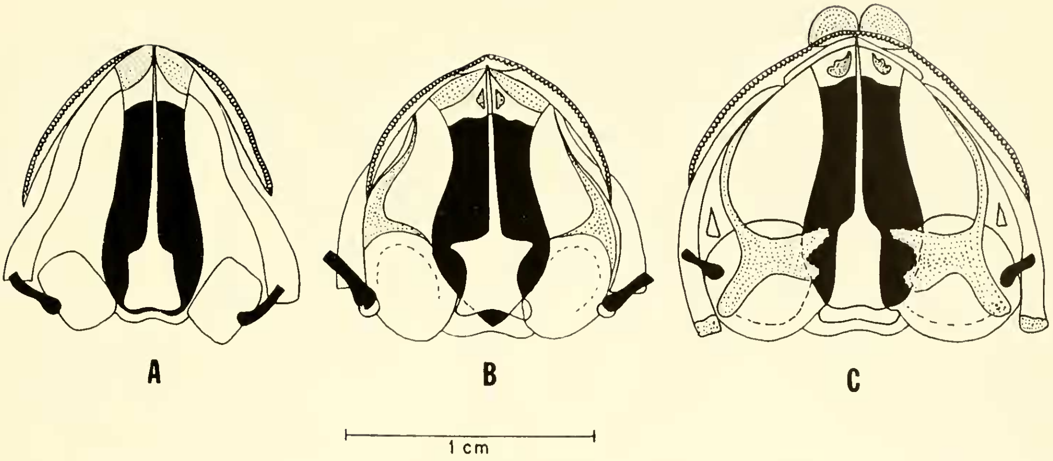


Figure 10. Reconstruction of the skulls of the three Ramon pipids. A. *Cordicephalus longicostatus;* B. *Cordicephalus gracilis;* C. *Thoraciliacus rostriceps.* Solid black and stippling are used to distinguish bones and do not imply the nature of substance.

monocondylar.

23) Four pairs of free ribs corresponding to presacrals two through five.
24) Rib fusions with their corresponding transverse processes occasionally occur.
25) Successive vertebrae not fused.

PECTORAL GIRDLE (Fig. 12)

26) Pectoral girdle inferred arciferal.
27) Clavicles and coracoids strongly divergent.
28) Coracoids with strong shafts expanded at both ends.
29) Clavicles large and strongly arched.
30) Clavicles and coracoids meet midventrally.
31) Scapula small and mostly uncleft.
32) Suprascapula a large petaloid blade.
33) Cleithrum large, V-shaped.
34) Sternum, episternum and coracoidal cartilages absent.

PELVIC GIRDLE (Fig. 11)

35) Pubis ossified.
36) Ilia long in *Thoraciliacus*, relatively short in *Cordicephalus.*
37) Pelvic articulation either iliocostal (= medioiliac, in *Thoraciliacus*) or acroiliac (in *Cordicephalus*).
38) Ischium relatively long.
39) Epipubis absent.

FORELIMB (Fig. 13)

40) Humerus straight, mostly smooth, having a well-developed spherical capitate eminence.
41) Radioulna single, flat, expanded at both ends, having a prominent olecranon.
42) Nine free carpals.
43) Four fingers with very long metacarpals, 2, 2, 3, 3 phalanges, the terminals being pointed.
44) Prepollex represented by its carpal only.

HINDLIMB (Fig. 13).

45) Femur faintly S-shaped, having a low, short femoral crest.
46) Tibiofibula single, strong, slightly shorter than the femur.
47) Tibiale and fibulare are elongated, fused at the two ends.
48) Five free distal tarsals.
49) Five toes with very long metatarsals,

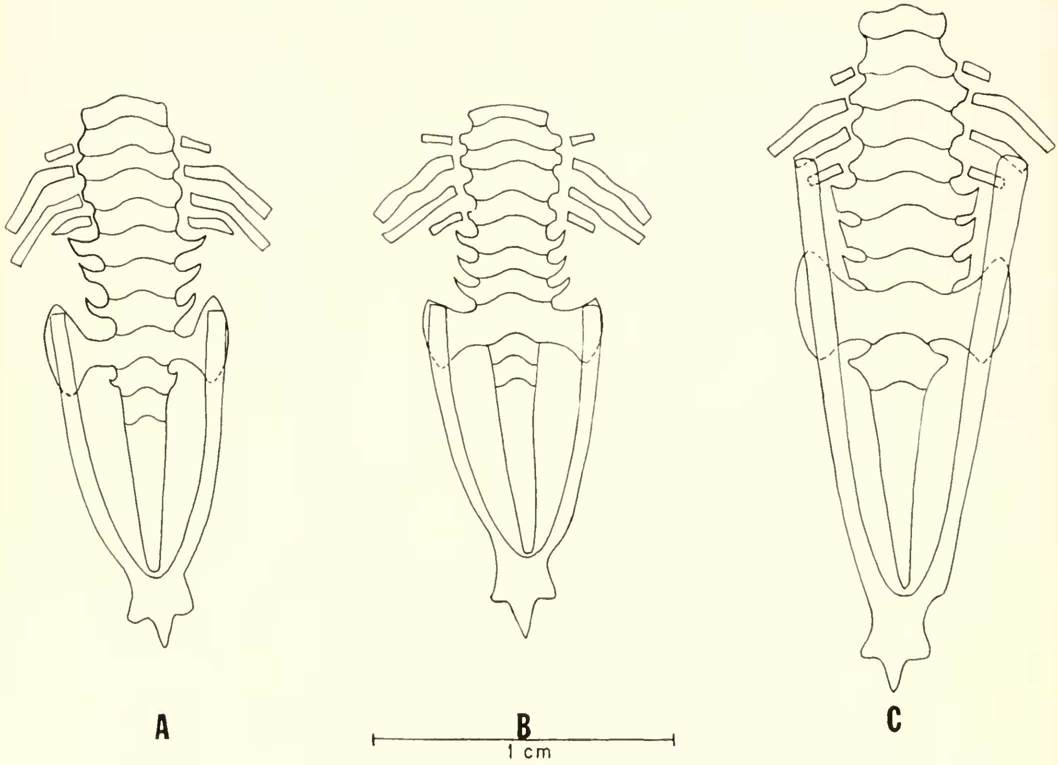


Figure 11. Reconstruction of the vertebral column and pelvis of the three Ramon pipids. A. *Cordicephalus longicostatus*; B. *Cordicephalus gracilis*; C. *Thoraciliacus rostriceps*.

2, 2, 3, 4, 3 phalanges, the terminals being pointed.

50) Prehallux represented by a metatarsal in *Cordicephalus*, but only by a tarsal in *Thoraciliacus*.

51) Epiphyses of long bones well ossified.

VARIATION

Both inter- and intra-populational variations are evident in the three sympatric populations of Ramon frogs. The morphological differences described above (diagnoses, Table 6, 7, and Figs. 4–13) provide the qualitative taxonomic differential evidence. Statistically significant differences of several variates (Tables 4, 5; Fig. 16), support the qualitative deductions. The *interpopulational* qualitative and quantitative differences are explicable only on the assumption of three coexisting related taxa, and rule out any sex or age alternative explanations.

The availability of large samples, particularly for *Thoraciliacus*, permitted the study of intrapopulational variation of size, shape, and meristic characters in Ramon frogs. The detailed study will be reported elsewhere. All three Ramon samples are homogeneous as regards place, environment, and time, but heterogeneous with regard to sex, age, and individuals. Meristic variations appear in Figure 14, and size-shape variations of the vertebral column and pelvis in Figure 15.

The univariate statistics of the three populations are shown in Table 3. The coefficients of variation ($V = 100\ s\ \bar{x}$) are averaged for all variates and for each skeletal system of the three species in Figure 16.

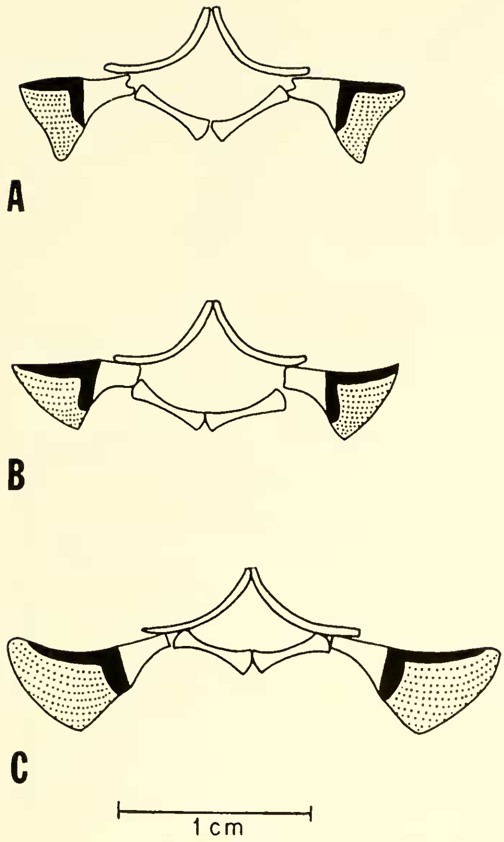


Figure 12. Reconstruction of the pectoral girdles of the three Ramon pipids. A. *Cordicephalus longicostatus;* B. *Cordicephalus gracilis;* C. *Thoraciliacus rostriceps.* The cleithrum is indicated in block; the suprascapula is stippled.

Skull. Shape variation is prominent in the frontoparietals, columella, and particularly in the squamosals. Remarkable individual variation is found in the frontoparietals. Four out of 62 specimens, or 6.5 per cent, of *Thoraciliacus* have a median suture in these usually azygous bones (e.g. in F 42, 32, 148 ?, 258). A small median oval foramen in specimens F 14, 54 ?, 56, 341 might represent the parietal foramen, which may not have been preserved in other specimens. Numerous small round holes show in each of the frontoparietals of six specimens (F 42, 45, 98, 133, 134, 213). Their nature is obscure. Teeth vary in number in the maxilla (33–37; mean = 35), and premaxilla (8–10).

Vertebral column (Figs. 11, 14, 15). Size, shape, and meristic variation are evident in each part of the column but are most striking in the urostyle. Eight presacrals characterize all three species, yet one or two specimens (F 112, on Fig. 15, and 127 ?) out of 256, or 0.8 per cent, have nine presacrals. All analyzable centra proved opisthocoelous in 261 skeletons, but many vertebrae are not determinable. The sacral diapophyses in 239 out of 250, or 95.6 per cent, are symmetrically attached to the ninth vertebra. The remaining 11 specimens display individual variation of right-left asymmetry of the diapophyses on the ninth vertebra only, or involving the 8th, and 10th vertebrae, as well (Figs. 14, 15). Successive vertebrae are not fused throughout the column. Ribs display striking individual variations in shape, size, and direction, and presumably age variation in fusions with their diapophyses. The older the animal the more fusions occur, particularly in ribs 1 and 4. The atlas is normally ribless, yet in 17 out of 232 cases, or 7.3 per cent, it has small and simple ribs or just diapophyses (Fig. 15, F 60). The second rib of *Thoraciliacus* is the longest in 138 out of 181 cases. In 43 specimens, or 23.75 per cent, the third is the longest. The urostyle may be wide and short or long and narrow. The proximal portion tends as a rule to have postsacral vertebrae, diapophyses or both. Out of 184 cases, 178, or 96.73 per cent, display postsacrals; the rest are apparently smooth indivisible rods. In *Thoraciliacus*, 140, or 76.08 per cent, have one postsacral, with or without diapophyses. In *Cordicephalus*, 3 out of 9, or 68.4 per cent, have two postsacrals; for other variations and their frequencies, involving up to four postsacrals, refer to Figures 14 and 15, and Plate 6 B.

Pectoral girdle (Fig. 12). The scapula is the most variable component of the pectoral girdle of the three species. Normally its proximal margin is uncleft; yet cleft

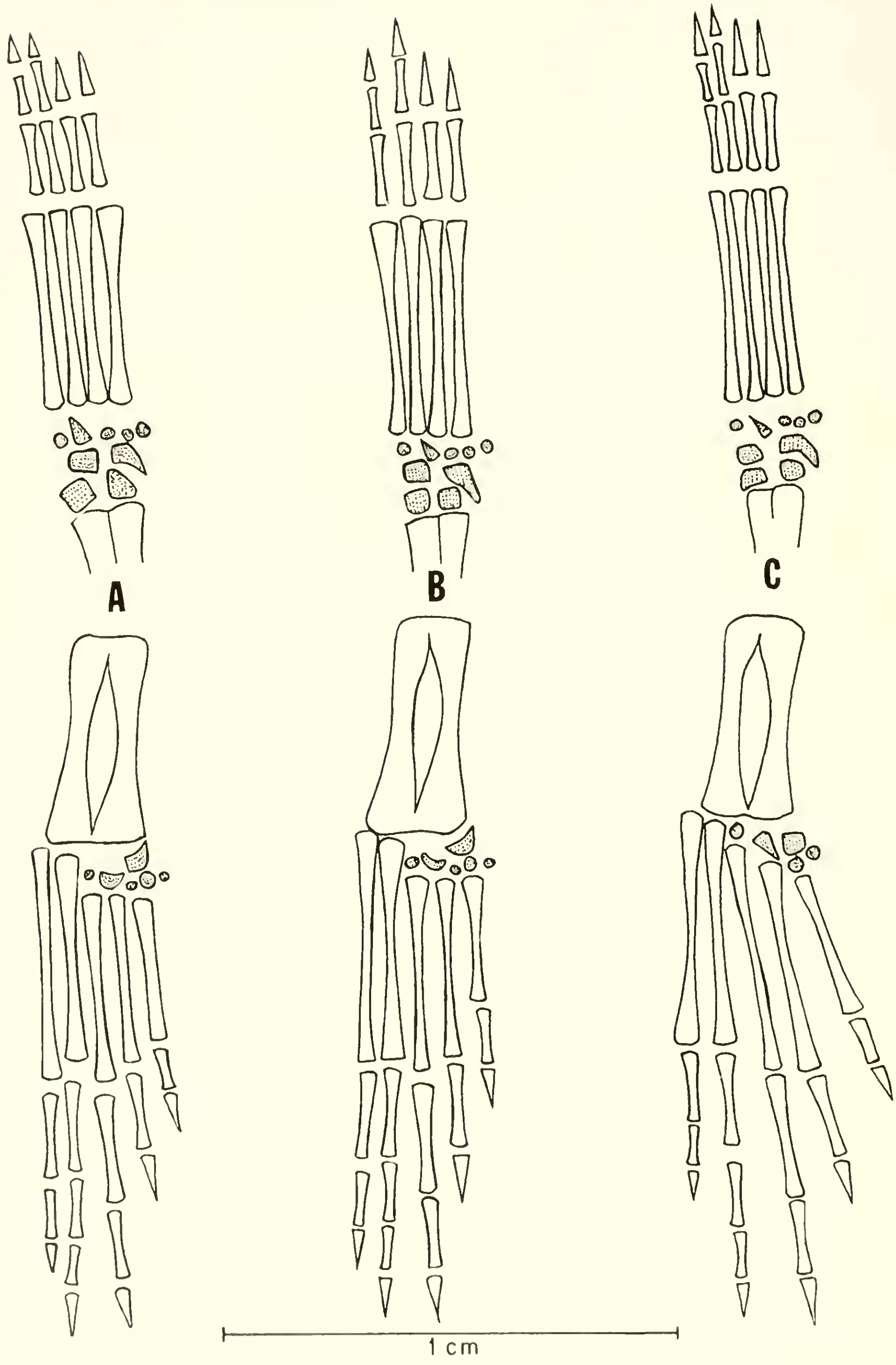


Figure 13. Reconstruction of the manus (upper three drawings), and pes and tarsus (lower three drawings) of the three Ramon pipids. A. *Cordicephalus longicostatus*; B. *Cordicephalus gracilis*; C. *Thoraciliacus rostriceps*.

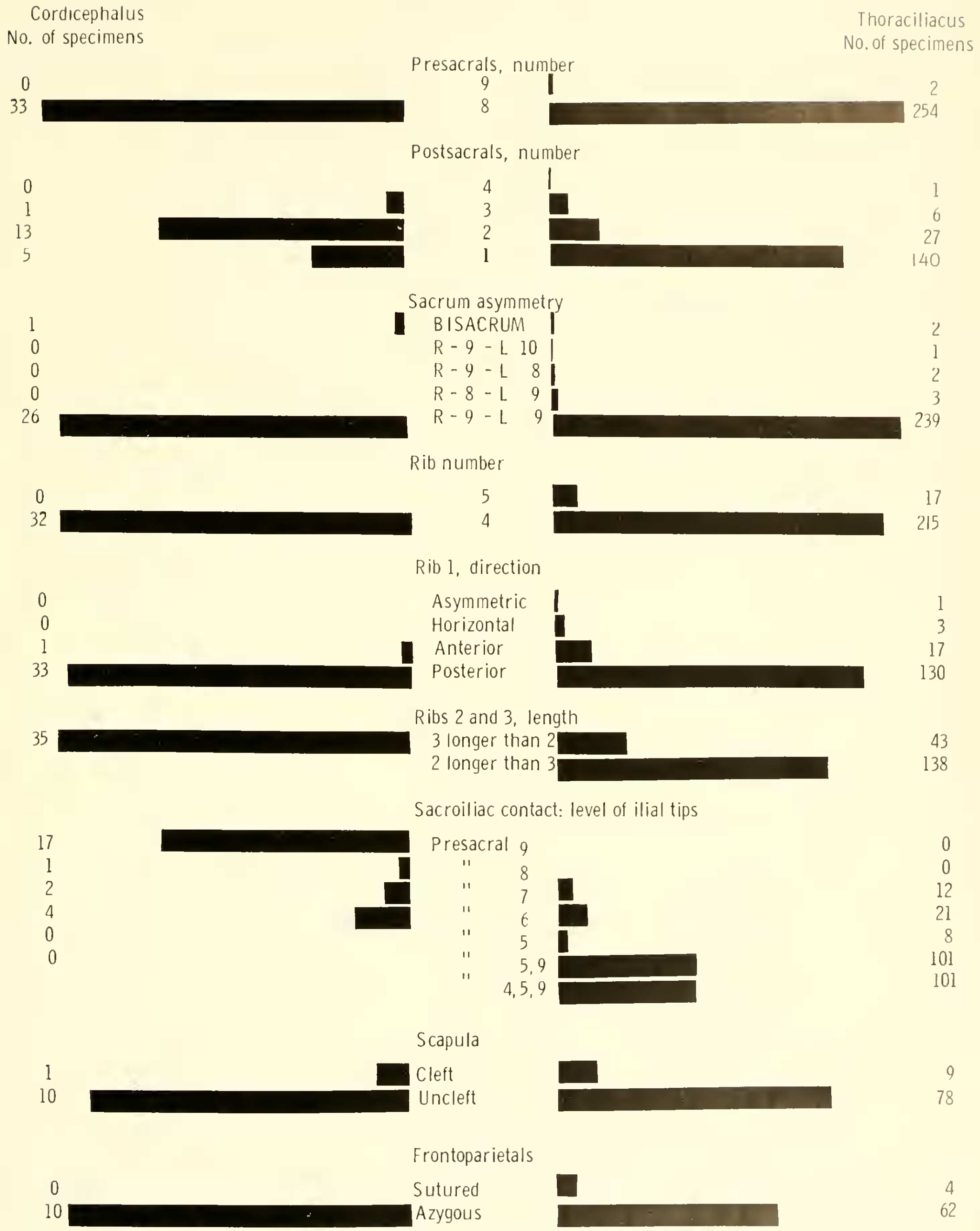


Figure 14. Meristic variations in *Thoraciliacus rostriceps* and *Cordicephalus gracilis*. Horizontal bars indicate percentages; the numbers on the right and left sides are of specimens. Figure 15 shows some of the variants whose frequencies appear above.
)

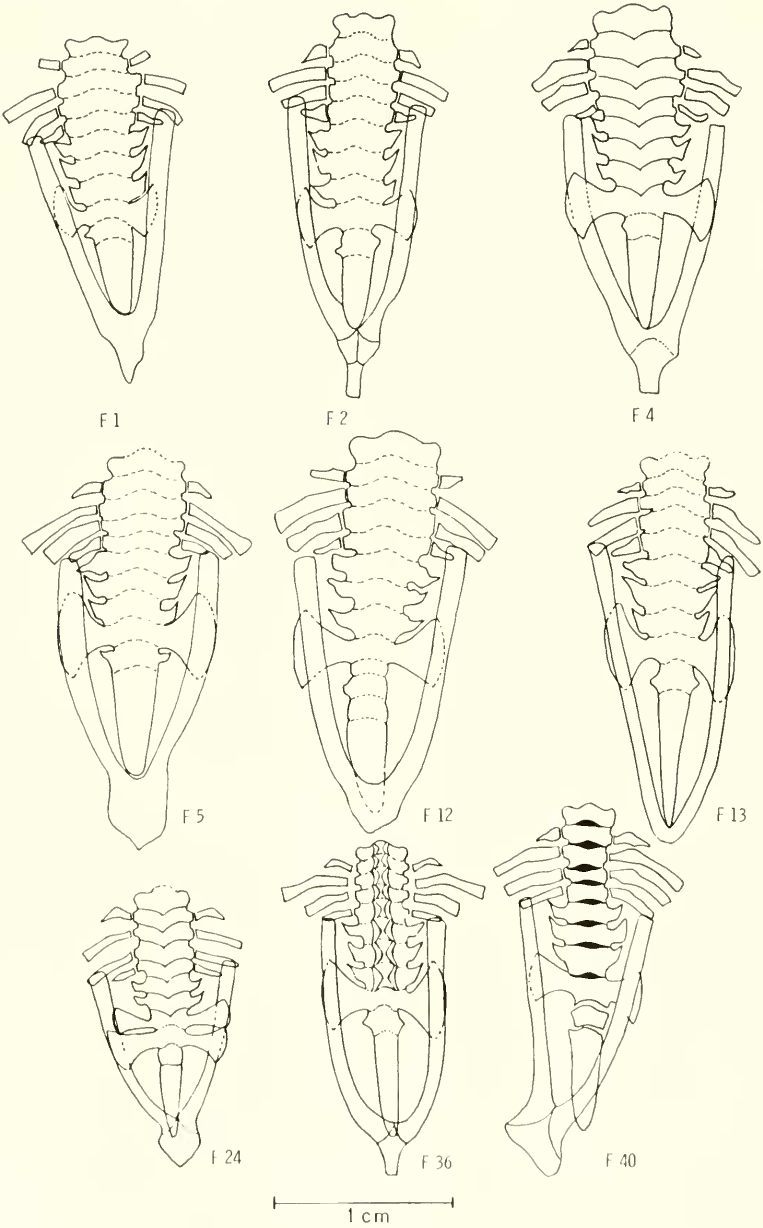
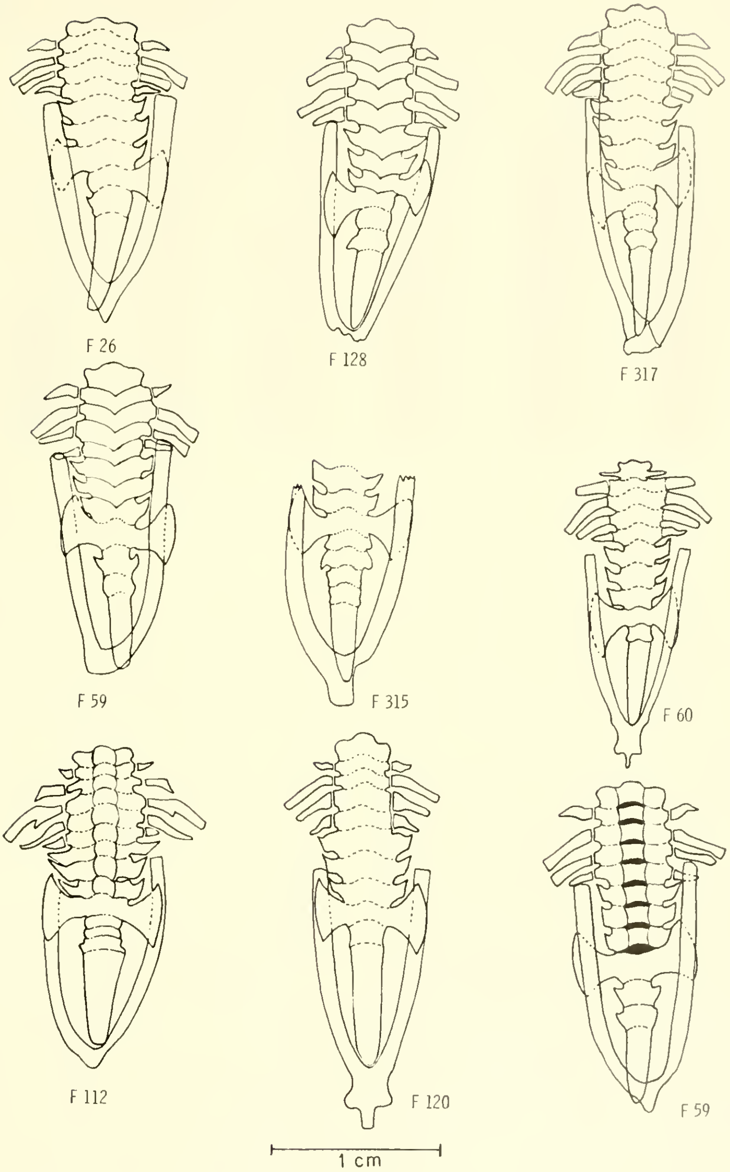


Figure 15. Variations in the vertebral column and pelvis of *Thoraciliacus rostriceps*. For frequencies of the presented cases refer to Figure 14. Note variation in shape of ribs, ilia, sacrum, urostyle. F 1—iliocostal articulation; ilia contact extensions of presacrals 4, 5, 9. F 2—iliocostal articulation as for F 1; note puboischium complex. F 4—dorsal aspect; iliocostal articulation, the ilia contact the extensions of presacrals 5, 9. F 5—rib 2 longer than 3; postsacral with diapophyses. F 12—three postsacrals. F 13—asymmetry of sacral diapophyses on vertebra 9. F 24—bisacrum. F 36—ecto-



chordal centra. F 40—black indicates matrix; note asymmetry of sacral diapophyses. F 26—sacral asymmetry: right sacral diapophysis on vertebra 9; left sacral diapophysis on vertebra 8; abbreviated on Figure 14 to: R-9–L-8. F 128—sacral asymmetry: R-8–L-9. F 317—sacral asymmetry: R-9–L-10. F 59—two postsacrals; asymmetry of rib one. F 315—four postsacrals. F 60—five ribs (additional rib on the atlas). F 112—five ribs; nine presacrals; three postsacrals. F 120—tips of ilia reach level of presacral seven. F 59—counterpart; black indicates matrix; two postsacrals with diapophyses.

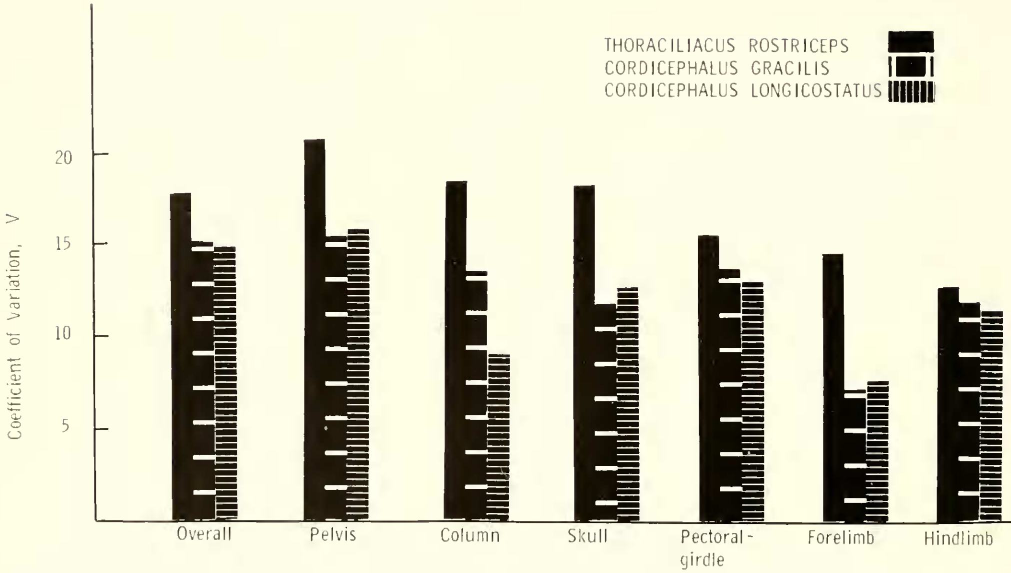


Figure 16. Mean V, coefficient of variation, of the three Ramon species, for the whole skeleton, and for each skeletal system.

scapulae show in 9 out of 78 cases, or 11.5 per cent, of *Thoraciliacus*; in 1 out of 11 in *Cordicephalus gracilis*, and in all of the three analyzable cases of *C. longicostatus* (Pl. 11 E).

Pelvic girdle (Figs. 11, 14, 15). The pelvic articulation is highly variable in *Thoraciliacus*. The tips of the ilia make contact with ribs 3 and 4 (Pl. 6 A) in 101 out of 243 cases, or 41.6 per cent, and with only the 4th rib (Pl. 6 E) in another 41.6 per cent, amounting to 83 per cent iliocostal contact in all. In the remaining 17 per cent the ilia end freely at the level of presacrals 5, 6, and 7 (Pl. 4). The great variation is reflected in the high V of presacral ilium of 26.93 (Table 3).

Limbs. The limbs display the least meristic and continuous variation in the whole skeleton (Figs. 13, 16).

In summary, *Thoraciliacus* is more variable than *Cordicephalus* in both meristic and continuous variations (Figs. 14, 16). The coefficient of variation (V) is 18.05 in *Thoraciliacus rostriceps* (average of 28 variates), versus 15.90 in *Cordicephalus gracilis*, and 15.75 in *C. longicostatus* (average of 25 and 24 variates respectively). The different skeletal systems within a species display differential amounts of variation. In all three species the pelvis is the most, the limbs are the least, variable. Other skeletal systems differ in order of decreasing amount of variations among the three species (Figure 16).

DISCUSSION

Relationships and Evolutionary Interpretation of Ramon Frogs

General. The characters listed in the osteological summary indicate that the three Ramon species are closely related and may be referred to the same family. Each skeletal system will now be evaluated for taxonomic relationships, variation, adaptation, and phylogeny, in order to assess the evolutionary significance of Ramon frogs. The evaluation of the taxonomic criteria and their significance is largely based on the critical review of Griffiths (1963).

The precise Paleozoic ancestry of Anura is uncertain (Parsons and Williams, 1963),

TABLE 2. MEASUREMENTS IN MILLIMETERS OF THE TYPE SPECIMENS

Variate	*Thoraciliacus rostriceps* HUJZ No. F 93	*Cordicephalus gracilis* HUJZ No. F 165	*Cordicephalus longicostatus* HUJZ No. F 171
Head + body length	41.4	30.3	31.0
Skull length	14.5	10.6	11.8
Skull width	14.5	12.0	11.5
Otic capsule length	5.0	5.1	5.0
Otic capsule width	4.2	3.4	3.0
Vertebral column length	11.6	9.0	10.5
Urostyle length	11.0	7.8	9.4
Humerus length	11.0	9.2	10.0
Radioulna length	8.4	6.2	7.3
Metacarpalia length	6.2	5.0	5.8
Clavicle length	6.2	–	–
Coracoid length	4.6	–	4.9
Scapula length	3.6	3.0	2.9
Scapula width	2.4	2.2	2.5
Femur length	13+	12.8	13.0
Tibiofibula length	–	12.2	13.0
Tibiale-fibulare length	–	5.0	5.6
Metatarsalia length	–	6.6	6.0
Sacral diapophysis length	4.1	4.1	4.0
Sacral diapophysis width	3.0	2.9	2.4
Puboischium length	4.4	2.8	3.6
Presacral ilium length	3.6	0.7	–
Ilium length	17.4	11.0	12.2

SPECIFICATION OF MEASUREMENTS.

Head + body length. The distance from tip of snout to tip of ischium.

Skull length. The distance from tip of snout to posterior margin of exoccipital condyles.

Skull width. The maximum distance between the outer margin of the prearticular along a line normal to mid-otic capsules.

Vertebral column length. The distance from tip of atlas to tip of sacrum.

Clavicle length. The least distance between tips of clavicles.

Scapula length. The total distance of the diagonal outer margin of scapula.

Scapula width. The minimum distance between the anterodistal point of scapula to the proximal uncleft margin.

Sacral diapophysis width. The distance from the lateral margin of the centrum to the distal margin of the diapophysis along a line normal to the centrum.

Puboischium length. The distance from tip of pubis to tip of ischium.

TABLE 2. *Continued*

Ilium presacral length. The length from the anterior tip of the sacral diapophysis to the anterior tip of the ilium.

All other dimensions are the maximum distances between parallel planes tangential to the designated anatomical elements: urostyle, humerus, radioulna, metacarpal, metatarsal, tibiofibula, tibiale-fibulare, etc.

yet amphibamids (Griffiths, 1963, and his references; Estes, 1965) or branchiosaurids (Noble, 1931; Reig, 1964) are possible ancestors. On the other hand, the early Triassic *Triadobatrachus* (= *Protobatrachus*, name preoccupied, Kuhn 1962) seems to be a plausible proanuran ancestor (Griffiths, 1963; Tihen, 1965), despite some recent doubts (Hecht, 1962). The earliest known true frog, *Vieraella herbstii* Reig, from the early Jurassic of Argentina indicates that the anuran grade evolved in pre-Jurassic times. The still undocumented transition from proanurans to anurans took place presumably during the Triassic. In the following discussion I will refer to labyrinthodonts, *Triadobatrachus*, and Jurassic frogs as the points of reference by which to distinguish primitive from specialized characters. All references to *Triadobatrachus* and *Notobatrachus* are to Piveteau (1937) and Reig (1957), respectively, unless otherwise specified.

Skull. The skulls of the three Ramon species have many more features in common than those separating them. This is evident from the similarities given in the osteological summary and the differences as shown in Table 6. The differences are either specific or, at most, generic in rank.

In most characters the skulls of all three species agree with the skulls of Recent pipids (Paterson, 1939, 1945, 1955, 1960). The character complex indicative of pipid affinities comprises: *azygous frontoparietals; developed columella; large otic capsules; an incomplete maxillary arcade; reduced maxillae, vomers, and squamosals;*

TABLE 3. MEASUREMENTS OF *THORACILIACUS ROSTRICEPS*, *CORDICEPHALUS GRACILIS*, AND *CORDICEPHALUS LONGICOSTATUS*, IN MILLIMETERS

Variate	N	Range	Mean ($\bar{x}$)	Standard Error ($S_{\bar{x}}$)	Standard Deviation (s)	Coefficient of Variation (V)
A. *Thoraciliacus rostriceps*						
Head + body length	118	20.5–51.5	32.49	0.49	5.38	16.56
Skull length	126	6.6–17.0	12.05	0.17	1.95	16.24
Skull width	122	9.2–18.2	12.79	0.15	1.76	13.76
Otic capsule length	140	2.4– 6.9	4.32	0.06	0.81	18.92
Otic capsule width	141	2.6– 6.8	4.21	0.06	0.80	18.98
Orbit length	88	2.8– 8.4	5.53	0.13	1.06	19.21
Orbit width	88	1.4– 5.2	3.01	0.08	0.75	25.05
Interorbital space	64	2.5– 6.5	4.05	0.12	0.97	23.94
Vertebral column length	170	7.0–17.8	11.01	0.13	1.78	16.17
Urostyle length	121	5.0–12.4	8.03	0.15	1.70	21.19
Urostyle width	105	1.0– 3.3	2.02	0.04	0.45	22.60
Puboischium length	82	1.2– 5.6	2.90	0.08	0.78	27.18
Humerus length	158	6.4–13.0	9.65	0.11	1.41	14.65
Radioulna length	138	4.4– 9.3	6.76	0.08	1.02	15.10
Metacarpalia length	84	4.0– 7.9	5.72	0.09	0.88	15.46
Clavicle length	42	3.3– 6.6	4.79	0.12	0.78	16.30
Coracoid length	74	3.0– 6.3	4.39	0.07	0.63	14.35
Scapula length	105	1.7– 4.2	3.04	0.05	0.50	16.59
Scapula width	100	1.5– 3.5	2.45	0.04	0.43	17.86
Femur length	114	10.0–19.0	13.47	0.14	1.60	11.88
Tibiofibula length	88	9.5–16.7	13.00	0.17	1.61	12.44
Tibiale-fibulare length	69	4.0– 8.8	6.18	0.11	0.96	15.56
Metatarsalia length	52	4.3– 8.3	6.40	0.11	0.85	13.28
Sacral diapophysis length	138	2.4– 6.7	3.92	0.06	0.78	19.92
Sacral diapophysis width	142	1.2– 4.4	2.55	0.04	0.50	19.64
Ilium length	138	9.0–19.6	13.72	0.17	2.08	15.25
Ilium presacral length	147	1.0– 6.7	3.25	0.07	0.87	26.93
Ilium width	125	0.7– 1.7	1.07	0.01	0.22	20.59
B. *Cordicephalus gracilis*						
Head + body length	30	22.5–31.5	26.05	0.42	2.32	8.92
Skull length	21	8.4–11.7	9.87	0.22	1.03	10.53
Skull width	17	8.7–13.0	10.63	0.32	1.35	12.76
Otic capsule length	32	3.3– 5.1	4.14	0.08	0.50	12.10
Otic capsule width	34	3.0– 4.4	3.76	0.07	0.41	11.06
Orbit length	12	3.6– 6.0	4.70	0.20	0.69	14.68
Orbit width	12	2.1– 3.5	2.71	0.12	0.44	16.37
Vertebral column length	41	7.4– 9.8	8.69	0.08	0.50	5.76
Urostyle length	24	4.7– 8.8	6.70	0.23	1.17	17.49
Urostyle width	28	1.0– 2.4	1.51	0.05	0.29	19.35
Puboischium length	13	1.3– 2.8	2.10	0.12	0.50	21.38
Humerus length	26	7.5–10.0	8.70	0.11	0.60	6.94
Radioulna length	23	5.2– 7.0	6.20	0.11	0.56	9.05
Metacarpalia length	17	3.8– 6.2	4.98	0.15	0.65	13.09
Clavicle length	2	3.6– 4.5	4.05	0.45	0.63	15.71
Coracoid length	14	3.1– 5.2	4.07	0.16	0.59	14.65
Scapula length	15	2.0– 3.0	2.48	0.09	0.35	14.15
Scapula width	16	1.7– 2.7	1.90	0.06	0.25	13.45
Femur length	20	10.0–13.8	11.40	0.26	1.18	10.39
Tibiofibula length	17	9.8–13.2	11.10	0.23	0.96	8.69
Tibiale-fibulare length	16	4.3– 6.2	5.15	0.13	0.55	10.69
Metatarsalia length	14	4.5– 6.7	5.89	0.17	0.63	10.82

TABLE 3. *Continued*

Variate	N	Range	Mean ($\bar{x}$)	Standard Error ($S_{\bar{x}}$)	Standard Deviation (s)	Coefficient of Variation (V)
Sacral diapophysis length	33	2.7– 4.6	3.45	0.08	0.49	14.21
Sacral diapophysis width	36	2.1– 3.3	2.65	0.05	0.31	11.89
Ilium length	26	8.2–11.8	10.21	0.19	0.97	9.57
Ilium presacral length	22	0.0– 1.7	0.42	0.11	0.52	–
Ilium width	26	0.7– 1.2	0.92	0.02	0.12	13.84
C. *Cordicephalus longicostatus*						
Head + body length	9	28.0–33.0	31.44	0.55	1.66	5.30
Skull length	6	9.0–11.9	10.40	0.48	1.20	11.52
Skull width	4	11.5–12.5	12.00	0.20	0.40	3.40
Otic capsule length	10	3.5– 5.0	4.31	0.15	0.48	11.23
Otic capsule width	9	3.0– 5.0	3.85	0.25	0.76	19.93
Orbit length	3	5.6– 7.0	6.36	0.40	0.71	11.14
Orbit width	2	4.0– 4.6	4.30	0.30	0.42	9.87
Vertebral column length	14	9.0–12.0	10.15	0.20	0.78	7.74
Urostyle length	8	8.0– 9.9	8.95	0.21	0.60	6.78
Urostyle width	10	1.5– 2.3	1.71	0.07	0.23	13.91
Puboischium length	6	2.5– 4.3	3.28	0.25	0.61	18.82
Humerus length	12	8.5–12.0	10.19	0.28	0.98	9.65
Radioulna length	10	6.1– 8.5	7.44	0.22	0.71	9.68
Metacarpalia length	8	5.3– 6.0	5.61	0.10	0.29	5.25
Clavicle length	1	5.3	5.30	–	–	–
Coracoid length	7	3.5– 4.9	4.21	0.19	0.50	12.05
Scapula length	5	2.3– 3.0	2.70	0.14	0.32	12.00
Scapula width	4	2.1– 2.5	2.27	0.08	0.17	7.51
Femur length	6	11.0–13.0	12.23	0.29	0.70	5.80
Tibiofibula length	4	10.1–13.0	11.90	0.69	1.39	11.70
Tibiale-fibulare length	3	5.3– 5.8	5.56	0.14	0.25	4.52
Metatarsalia length	2	5.5– 6.0	5.75	0.25	0.35	6.15
Sacral diapophysis length	9	3.2– 4.3	3.72	0.11	0.35	9.38
Sacral diapophysis width	10	2.4– 3.8	3.07	0.12	0.40	13.03
Ilium length	11	9.7–12.6	11.71	0.25	0.84	7.19
Ilium presacral length	8	0.0– 2.5	0.48	0.33	0.94	–
Ilium width	10	1.0– 1.4	1.13	0.05	0.16	14.48

absence of palatines, quadratojugals, and mentomandibulars; and ossified quadrates. Each isolated character may appear, and vary distinctly, in other families; only the assemblage implies pipid allocation.

Azygous frontoparietals, though universal in pipids, were described also for *Hemisus, Pelobates, Rhinophrynus,* and *Palaeobatrachus.* It is noteworthy that these are either fossorial or aquatic forms. The presence of a suture in the frontoparietals of the Cretaceous *Eoxenopoides*, *Saltenia*, and possibly *Shelania* was incorporated in the diagnosis of the new pipoid family Eoxenopoididae (Casamiquela, 1961a). Yet paired frontoparietals are displayed by premetamorphic *Xenopus* (Sedra and Michael, 1958), and a median suture is a variable character in *Thoraciliacus* (Fig. 14). Hence both embryology and variation speak against high taxonomic significance for the divided condition, and the character is better included within pipid developmental patterns and variational range.

Ear. Most anurans have complete middle ear bones. Occasionally, however, the columella is missing and only the operculum remains. The latter condition is a feature of the following random assemblage of anurans: *Phryniscus, Hemisus, Cacosternum, Brachycephalus, Pelobates, Rhinophrynus, Bombina,* and ascaphids.

Table 4. Student's *t*-tests Between the Sample Means of the Two Genera *Thoraciliacus* and *Cordicephalus*

	Thoraciliacus			*Cordicephalus*					
Variate	N	Mean	Standard Deviation	N	Mean	Standard Deviation	Student's t	Degrees of Freedom	P
Head + body length	118	32.49	5.38	39	27.29	3.16	5.705	155	<.001
Skull length	126	12.05	1.95	27	9.99	1.07	5.293	151	<.001
Skull width	122	12.79	1.76	21	10.89	1.34	4.713	141	<.001
Orbit length	88	5.53	1.06	15	5.03	0.96	1.697	101	.1
Orbit width	88	3.01	0.75	14	2.94	0.71	0.313	100	.7–.8
Otic capsule length	140	4.32	0.81	42	4.18	0.49	1.058	180	.2–.3
Otic capsule width	141	4.21	0.80	43	3.78	0.50	3.349	182	<.001
Vertebral column length	170	11.01	1.78	55	9.06	0.86	7.823	223	<.001
Urostyle length	121	8.03	1.70	32	7.26	1.44	2.328	151	.02
Urostyle width	105	2.02	0.45	38	1.56	0.29	5.775	141	<.001
Puboischium length	82	2.90	0.78	19	2.47	0.74	2.155	99	.02–.05
Humerus length	158	9.65	1.41	38	9.17	1.01	1.978	194	.05
Radioulna length	138	6.76	1.02	33	6.57	0.83	0.977	169	.3–.4
Metacarpalia length	84	5.72	0.88	25	5.18	0.63	2.829	107	.01–.001
Clavicle length	42	4.79	0.78	3	4.46	0.85	0.701	43	.4–.5
Coracoid length	74	4.39	0.63	21	4.12	0.56	1.794	93	.05–.1
Scapula length	105	3.04	0.50	20	2.53	0.34	4.300	123	<.001
Scapula width	100	2.45	0.43	20	1.97	0.28	4.712	118	<.001
Femur length	114	13.47	1.60	26	11.59	1.13	5.658	138	<.001
Tibiofibula length	88	13.00	1.61	21	11.25	1.06	4.711	107	<.001
Tibiale-fibulare length	69	6.18	0.96	19	5.22	0.53	4.177	86	<.001
Metatarsalia length	52	6.40	0.85	16	5.87	0.60	2.310	66	.02
Sacral diapophysis length	138	3.92	0.78	42	3.51	0.47	3.197	178	>.001
Sacral diapophysis width	142	2.55	0.50	46	2.74	0.37	2.409	186	.01–.02
Ilium length	138	13.72	2.08	37	10.65	1.16	8.577	173	<.001
Ilium presacral length	147	3.25	0.87	30	0.43	0.64	16.679	175	<.001
Ilium width	125	1.07	0.22	36	0.98	0.16	2.385	159	.01–.02

The correlation between the absence of the columella and fossorial habits (Eiselt, 1941), either in terrestrial or marginal aquatic habitats, may prove significant, but it needs further evidence. Conversely, pipids have a remarkably developed columella, suggesting its efficacy in purely aquatic habitats.

Most Jurassic and Cretaceous frogs have a columella, indicating its primitiveness in Anura. The *Notobatrachus* case is as yet unsettled (see Casamiquela, 1961a, b, and Hecht, 1963, for negative and positive statements, respectively). Ramon frogs have a large columella linked, at least in *Cordicephalus*, with an operculum, as in Recent *Xenopus*. Presence of middle ear bones appears to be primary, hence primitive.

Extensive otic capsules, varying only in degree, are a feature of all pipoids. Large capsules as an exclusive eoxenopoidid character (Casamiquela, 1961a) are thus ruled out. Hecht (1963: 22) claims that enlarged otic capsules are a feature of "advanced tadpoles and metamorphosing individuals," but large otic capsules characterize all Ramon pipids and the capsule size is positively correlated with total length. The correlation coefficient in *Thoraciliacus* ($N = 80$) is 0.37 ($P < .001$). Hence the extensive otic capsules of pipoids increase in size with age and are not just an embryonic feature but rather a lifelong adaptation especially prominent in adults. Paterson (1960) suggested that the presence of a large otolith in the inner ear sacculus of pipids implied gravitational and

TABLE 5. STUDENT'S *t*-TESTS BETWEEN THE SAMPLE MEANS OF THE TWO SPECIES OF *CORDICEPHALUS*

	Cordicephalus gracilis			*Cordicephalus longicostatus*					
Variate	*N*	Mean	Standard Deviation	*N*	Mean	Standard Deviation	Student's *t*	Degrees of Freedom	*P*
Head + body length	30	26.05	2.32	9	31.44	1.66	6.449	37	<.001
Skull length	21	9.87	1.03	6	10.39	1.19	1.054	25	.3
Skull width	17	10.63	1.35	4	11.99	0.40	1.956	19	.05–.1
Orbit length	12	4.69	0.69	3	6.36	0.70	3.725	13	.01–.001
Orbit width	12	2.71	0.44	2	4.29	0.42	4.678	12	<.001
Otic capsule length	32	4.14	0.50	10	4.30	0.48	0.922	40	.3–.4
Otic capsule width	34	3.76	0.41	9	3.85	0.76	0.464	41	.6–.7
Vertebral column length	41	8.69	0.50	14	10.14	0.78	8.085	53	<.001
Urostyle length	24	6.70	1.17	8	8.94	0.60	5.140	30	<.001
Urostyle width	28	1.51	0.29	10	1.70	0.23	1.934	36	.05–.1
Puboischium length	13	2.09	0.44	6	3.28	0.61	4.752	17	<.001
Humerus length	26	8.70	0.60	12	10.19	0.98	5.738	36	<.001
Radioulna length	23	6.20	0.56	10	7.43	0.71	5.334	31	<.001
Metacarpalia length	17	4.98	0.65	8	5.61	0.29	2.562	23	.01–.02
Clavicle length	2	4.04	0.63	1	5.29	0.00	1.604	1	.3–.4
Coracoid length	14	4.07	0.59	7	4.21	0.50	0.514	19	.6–.7
Scapula length	15	2.47	0.35	5	2.69	0.32	1.234	18	.2–.3
Scapula width	16	1.89	0.25	4	2.27	0.17	2.755	18	.01–.02
Femur length	20	11.40	1.18	6	12.23	0.70	1.613	24	.1–.2
Tibiofibula length	17	11.09	0.96	4	11.89	1.39	1.379	19	.1–.2
Tibiale-fibulare length	16	5.15	0.55	3	5.56	0.25	1.242	17	.2–.3
Metatarsalia length	14	5.89	0.63	2	5.75	0.35	0.304	14	.7–.8
Sacral diapophysis length	33	3.45	0.49	9	3.72	0.40	1.509	40	.1–.2
Sacral diapophysis width	36	2.65	0.31	10	3.06	0.40	3.464	44	.001–.01
Ilium length	26	10.21	0.97	11	11.71	0.84	4.454	35	<.001
Ilium width	26	0.92	0.12	10	1.12	0.16	3.941	34	<.001
Ilium presacral length	22	0.41	0.52	8	0.48	0.94	0.255	28	.8

vibrational responses of the saccular macula. Van Bergeijk (1959) has experimentally demonstrated vibrational responses in the saccular macula due to otolith motions in *Xenopus* tadpoles. Finally, Witschi *et al.* (1953) suggested that the *Xenopus* ear is adapted to underwater sound by its thick adipose tympanal mesenchyme, as well as fit to perceive aerial sound waves that skim along the water surface. It seems possible that the greatly inflated otic capsules of pipoids house air-filled spaces similar to those found in clupeid and mormyrid fishes (Van Bergeijk, 1967) and function as resonators which amplify weak vibrations. Such amplificatory devices of acoustic and vibratory stimuli would be advantageous in water in which amplifying mechanisms of weak air-borne stimuli would be at a premium. It appears that the pipid ear is a specialized aquatic adaptation.

Reduction of some skull bones, such as squamosals and prevomers, is usually associated with great shape variation and is confirmed in Ramon frogs. Such variation may be linked with degenerating characters which have lost all function (Simpson, 1953). Absence of quadratojugals (resulting in an incomplete maxillary arcade) and palatines occurs in various unrelated anurans (Ramaswami, 1939). The absence of these bones seems to imply convergent paedomorphy (Griffiths, 1963) rather than phylogenetic relationship. Certainly all cases of reduced and absent bones are specialized, whether acquired by paedomorphy or by any other genetic mechanism.

A rostrum of variable size occurs in unrelated anurans, e.g., *Bufo typhonius*, *Bufo*

TABLE 6. SKULL DIFFERENCES OF THE THREE RAMON SPECIES

Species	Skull Outline[1]	Quadrate Region	Nasals	Otic Capsules
Thoraciliacus rostriceps	Spatulate-ovoid	Posterior	Kidney-shaped forming a prominent rostrum	Spherical
Cordicephalus gracilis	Heart-shaped	Anterior	Medium, crescentic no rostrum	Elliptical
Cordicephalus longicostatus	Heart-shaped	Anterior	Broad-ovoid small rostrum	Rectangular

[1] Slight shape differences characteristic of each species occur in the parasphenoid, sphenethmoid, frontoparietals, pterygoids.

granulosus, *Triprion petasatus*, *Pipa pipa*, and others. In several tropical species of *Leptodactylus* the rostrum is a sexual character, males using pointed snouts to dig nesting holes for the females. Also, various burrowing frogs have sharp narrow snouts evolved in parallel and convergent lines (Noble, 1931). Burrowing down to two feet depth was reported for *Hemipipa* (Johnson, 1952), suggesting the digging habits in some pipids. Thus the prominent rostrum of *Thoraciliacus* may have been utilized for burrowing in mud bottoms. The flat skull of Ramon frogs may also reflect an aquatic adaptation.

Pipoids share essentially the same skull architecture in spite of shape variation within and between taxa (Table 9). The shape of certain bones may partly indicate intergeneric affinities. The sword-like parasphenoid of Ramon frogs affiliates them with *Xenopus* but segregates them from the broad parasphenoid of *Pipa*, *Hymenochirus*, *Shelania*, and the dagger-shaped parasphenoid of *Eoxenopoides* and *Paleobatrachus*. On the other hand, broad nasals are shared by *Thoraciliacus*, "eoxenpoidids," paleobatrachids, *Hymenochirus* and *Pipa*, whereas *Cordicephalus* has medium-size nasals, approximating the narrow *Xenopus* nasals. *Cordicephalus* further shares with *Xenopus* the anteriorly placed quadrate region, and it seems probable that the former type of skull is morphologically ancestral to the latter. On the other hand, the prominent *Thoraciliacus* rostrum coupled with its pelvic specializations make this genus an unlikely ancestor of any Recent pipid.

The skull of Ramon pipids is highly specialized (Table 10) but does not basically differ from the highly specialized skulls of Recent pipids (Paterson, 1955). Judging from gross skull morphology it appears that pipid skulls have evolved little since early Cretaceous times, and their main evolution was presumably Triassic in age.

In summary, the pipid skull is definable by a character-complex. It is specialized to aquatic life by its flatness and large otic capsules and may be paedomorphic. The variations displayed by fossil and Recent pipoids are at most generic in rank and all may be referred to the Pipidae.

Vertebral column. The vertebral column of the three species is basically similar, consisting of eight opisthocoelous presacrals with four pairs of long free ribs (details in the osteological summary; refer to Table 9 for comparison with other pipoids). The three species differ in shape of ribs and diapophyses and in the number of postsacrals (Fig. 11). *Thoraciliacus* has stout ribs and triangular diapophyses in presacrals six through eight and one postsacral, whereas *Cordicephalus* has longer ribs, arcuate diapophyses and, as a rule, two postsacrals. As a whole, the column agrees with the vertebral column of Recent pipids (Noble, 1931; Smit, 1953, and works there cited). However, Ramon frogs are distinguished from all fossil and Recent pipoids by the following character-complex: *ectochordal vertebrae, one or two* *postsacrals, monocondylar sacro-urostylar articulation, and four pairs of free ribs.* Each of these characters alone or several combined may occur in other frogs, but the assemblage is unique to *Cordicephalus* and *Thoraciliacus.* The following discussion deals with several aspects of the column.

Presacrals. Non-ascaphoids normally have eight presacrals, with a few generic variants (for pipoids refer to Table 9; for other Anura see Noble, 1931). Thus the presence of eight presacrals in Ramon frogs excludes affinities with ascaphoids, which normally have nine presacrals in the Recent Ascaphidae (Ritland, 1955) as well as in the Jurassic Notobatrachidae (Reig, 1957). Neither the 0.8 per cent of *Thoraciliacus* specimens having nine presacrals (Figs. 14, 15) nor the less than 3 per cent of *Ascaphus* skeletons reported by Ritland to have eight presacrals violate this rule; they rather confirm it by being only individual variants. No correlation is obvious between the number of presacrals in *Anura* and the type of locomotion. Both terrestrial *Oreophrynella* and aquatic *Hymenochirus* have a synsacrum, hence six free presacrals (Noble, 1931). Phylogenetically, however, the number of presacrals, whether eight or nine, reflects an ancient conservative figure, associated presumably with the emerging anuran grade and developed presumably from the 16 or so presacrals of triadobatrachids. All Jurassic and Cretaceous frogs have one or the other of these numbers indicating their primitiveness in Anura.

Opisthocoely is invariable in all 261 studied columns of Ramon frogs. This confirms the constancy of opisthocoely displayed by Recent pipid frogs as opposed to frequent variations in other vertebral patterns (Griffiths, 1963). The articulation patterns of presacrals have been correlated with the mechanics of motion (Gadow, 1933). Thus it appears that terrestrial life involving leaping, walking and climbing forms puts a premium on procoely, whereas opisthocoely and amphicoely are mainly restricted to aquatic and some fossorial forms. However, this correlation is subject to exceptions in both directions and is not yet experimentally supported (Schaeffer, 1949). Phylogenetically, *Triadobatrachus* as well as the known Jurassic frogs are either amphicoelous or opithocoelous, an indication of the primitiveness of these patterns, which appear to have preceded procoely. Hecht's (1963) claim that Jurassic *Notobatrachus* is procoelous, in contrast to its reported amphicoely (Reig, 1957), is disproved by the newly collected amphicoelous notobatrachid material (Casamiquela, 1961b, and personal communication).

Anurans fall into three developmental groups in respect to their vertebral centra, which may be ectochordal, stegochordal, or holochordal (Griffiths, 1963). Ectochordy is a feature of *Triadobatrachus*, ascaphids and rhinophrynids; stegochordy of discoglossids and pipids; and holochordy of all other anurans. The central type is correlatable with the mode of locomotion. Ectochordy and stegochordy occur both in aquatic and burrowing forms such as ascaphids, discoglossids, pipids, rhinophrynids, and pelobatids. Contrariwise, holochordal or solid centra occur in almost all leaping, walking, and climbing terrestrial forms. Phylogenetically, the ectochordy and nonimbricate zygapophyses of Ramon frogs are replaced by stegochordy and imbricate zygapophyses in Recent pipids. Functionally, imbricate zygapophyses replace the centrum, which in the stegochordal condition merely links the bases of the neural arches (Griffiths, 1963). This evolution reflects the progressive adaptive improvement that pipids underwent in swimming efficiency. Evidently, ectochordy is primitive and preceded stegochordy and holochordy in anuran evolution. The first two central types typify the aquatic, the third one the terrestrial radiation of Anura.

Postsacrals. These are constantly present in Ramon frogs, in contrast to their infrequency in other anurans. *Thoraciliacus* has one, *Cordicephalus* two postsacrals as a rule, though some individual variants display three and four urostylar vertebrae (Figs. 14, 15). One to three postsacrals may occur individually in Anura, particularly in the primitive families but also in some bufonids and ranids; but they are never a constant feature as in Ramon frogs. Recent adult pipids lack postsacrals, though three urostylar vertebrae are seen in premetamorphic *Xenopus* (Hodler, 1949; Smit, 1953). Thus pipids have eliminated postsacrals from the adult stage during their evolution, as did most frogs. This trend is linked to the basic adaptations of Anura and to the replacement of the undulatory by the propulsive type of locomotion, as registered in the short trunk and urostyle evolution. *Triadobatrachus* had an articulated tail involving at least six vertebrae (Hecht, 1962). Articulated tails have been reported in tadpoles of Recent *Megophrys major* (Griffiths, 1956) and of Ramon pipids (Nevo, 1956). These two finds register developmentally and paleontologically the evolution of the urostyle by fusion of caudal vertebrae [with a single hypochord in *Megophrys major* as demonstrated embryologically by Mookerjee (1931)]. Ramon frogs retain evidence of the primitive condition in both larva and adult. Gradual elimination of postsacrals through urostylization marks the transition from the undulatory proanuran to the propulsive anuran type of locomotion. The monocondylar sacro-urostylar joint of Ramon frogs distinguishes them from Recent pipids where this region is fused. The urostylar joint by itself has little taxonomic importance, yet it becomes significant within a character-complex. The region is functionally important, being free and flexible in leaping frogs (Whiting, 1961), but fused in aquatic forms "in which no shock absorption is required" (Green, 1931). Phylogenetically, the free joint preceded the fused region as the comparison of Ramon and Recent pipids shows. The same applies to fusions between ribs with their diapophyses or successive presacrals. Again, Ramon pipids usually have free ribs and free presacrals, whereas adult Recent pipids are ribless and have occasional presacral fusions. *Triadobatrachus* and all Mesozoic frogs have a monovertebral sacrum indicating the primitive condition. Synsacra, either in Recent or in Tertiary frogs, are specialized, and so are the expanded sacral diapophyses in aquatic and burrowing frogs.

Rib evolution in Anura is now traceable by means of fossils. Five ribs characterize premetamorphic paleobatrachids, and occur in individual specimens in 7.3 per cent of the *Thoraciliacus* sample (Figs. 14, 15). Four ribs occur in *Notobatrachus*, three Ramon species, and apparently also in *Saltenia* and *Shelania* (Casamiquela, personal communication). They may occur also in some individuals of *Xenopus* (Hodler, 1949). Three ribs are the rule in Recent costate anurans, but most Recent frogs are ribless. The long pipid ribs are points of insertion for muscles associated with the sub-aquatic locomotion which is to be discussed later. On the other hand, riblessness is at a premium in terrestrial anurans.

In sum, the column of *Cordicephalus* and *Thoraciliacus* is, in a broad sense, pipid, yet closer to ancestral conditions, differing from Recent pipids by a character-complex involving eight primitive as against two specialized characters (Table 10).

Pectoral girdle. The three Ramon species share essentially the same arciferal girdle, allowing for slight shape and size variations (see osteological summary and Fig. 12). They closely agree with the Recent pipids, particularly in the xenopoid pectoral girdle (De Villiers, 1924, 1929), in the following characters: *diverging coracoids and clavicles* (= arcifery *sensu* Cope and Boulenger); *a small scapula mostly uncleft proximally* (Proctor, 1921); *a large, V-shaped cleithrum, and episternum absent.* The Ramon girdles, particularly, approach the xenopoid type in having arched, anteriorly directed clavicles, shaft-like coracoids, and distinctly large cleithra. They are distinguished from *Xenopus* by having much more arcuate clavicles, and coracoids more expanded at both ends, thus approaching the girdle of "eoxenopoidids" and paleobatrachids, e.g., the fossil pipoids.

Arcifery, small scapula and large cleithrum form an adaptive complex characterizing aquatic anurans. Arcifery is present in both aquatic and terrestrial anurans, but the association with a small scapula is exclusive to aquatic frogs. Small scapulae (clavicle to scapula ratio is greater than three) characterize pipids, ascaphids, and discoglossids. That ratio is less than two in all other (terrestrial) anurans and is probably to be correlated with the incorporation of the forelimbs into the active locomotory apparatus (Griffiths, 1963). It is noteworthy that *Hymenochirus*, the only firmisternal pipid, has also the relatively largest scapula in the family and is more terrestrial than the others (De Villiers, 1929), whereas some aquatic firmisternal forms (ranoids) have small scapulae (Hsiao, 1934). Further, a small scapula is typically associated with an uncleft proximal margin as in ascaphids and pipids. This is basically true for Ramon pipids, even though some ten per cent of the specimens have cleft scapulae (Fig. 14). Conversely, the long scapula is invariably cleft. *Triadobatrachus* and all known Mesozoic anurans share a small uncleft scapula. Thus the latter is primitive, and it appears to be associated with aquatic adaptation, whereas a long cleft scapula appears to be a terrestrial specialization.

Phylogenetically, arcifery appears to have preceded firmisterny, on the evidence of both the fossil record and comparative anatomy. *Triadobatrachus* had a pectoral girdle like that of *Ascaphus*, which is generally considered arciferal. All known Mesozoic frogs are probably in this sense arciferal. Reig's (1957) claim that *Notobatrachus* has a firmisternal pectoral girdle (and that hence that type is ancestral in Anura) was challenged by Eaton (1959) who compared it with the ascaphid girdle. In fact, all Recent primitive anurans are arciferal, whereas the advanced ranoids are firmisternal. The relatively large cleithra and clavicles of Ramon frogs are labyrinthodont characters and hence apparently primitive. De Villiers (1924, 1929) stressed the unique large cleithrum in *Xenopus*, and Aglossa generally, as opposed to the anterior small osseous seam in phaneroglossids. Regarding cleithrum size as of utmost importance in linking anurans and labyrinthodonts, he considered *Xenopus* more primitive than *Pipa*, partly on the ground of its larger cleithrum. Ramon pipids confirm his thesis. Lack of an episternum in *Triadobatrachus*, *Notobatrachus*, ascaphids and pipids, and its very small size in discoglossids indicate absence as a primitive feature.

The pectoral girdle of Ramon frogs is xenopoid and primitive both as a whole and as regards its six components (Table 10). The pipid girdle apparently has not changed significantly since early Cretaceous times and displays an ancestral aquatic adaptive-complex.

Pelvic girdle. All three Ramon species share a medium to long ischium and an *ossified* pubis; these features are indications of pipid affinities (Green, 1931, and his references). In other regards, the two Ramon genera differ basically in their pelves (Table 7). *Cordicephalus* approximates the xenopoid pelvis in its sacroiliac articulation, but lacks the epipubis. Conversely, *Thoraciliacus* matches "eoxenopoidids" in its medioiliac joint, but beyond that has an iliocostal contact in 83 per cent of the sample (Fig. 14), establishing a *functional* synsacrum.

Convergent origin of some anuran pelvic structures, such as an epipubis and synsacry, makes them unreliable taxonomic criteria at the familial level. The same, it appears to me, holds for the medioiliac articulation used as a diagnostic eoxenopoidid criterion (Casamiquela, 1961a). It has developed convergently in several lines, proves highly variable inter- and intraspecifically, and therefore is undiagnostic. Nor does it seem to be primitive, as contended

TABLE 7. DIFFERENCES BETWEEN THE PELVIS OF *CORDICEPHALUS* AND *THORACILIACUS*

Genus	Shape of Pelvis	Sacroiliac joint	Ilium Length / Head + Body Length*	
Cordicephalus	Triangular	Acroiliac No functional synsacrum	0.381	($N = 29$)
Thoraciliacus	Sub-parallel to triangular	Iliocostal or medioiliac Functional synsacrum	0.429	($N = 107$)

* Student's $t = 6.808$, for 134 degrees of freedom, $P < .001$.

by Reig (1957) and Casamiquela (1961a), but, rather, a specialized aquatic adaptation. Varied degrees of anterior iliac extension, or medioiliac articulation, show in some pipoids, such as eoxenopoidids, paleobatrachids, and *Thoraciliacus*, but not in others, e.g., *Cordicephalus* and Recent adult pipids. There is little indication of it in *Notobatrachus* and *Ascaphus*. The character has been reported for premetamorphosed and just metamorphosed *Rana temporaria* (Green, 1931) and similar stages in *Xenopus laevis* (Guardabassi, 1955; personal unpublished observations) but is not known for their adults. The character is extremely variable in *Thoraciliacus*, displaying varied degrees of anterior extension (Fig. 14), and a high V of 26.93 as against the average V of 18.05 (Fig. 16). The so-called "morphological stages" of *Eoxenopoides* (Haughton, 1931) seem to reflect individual variations similar to those in *Thoraciliacus* rather than progressive morphological series.

The medioiliac joint and expanded sacral diapophyses are explicable as an aquatic-burrowing adaptive complex. In *Xenopus* the sacroiliac joint is movable, the ilia slide freely backwards and forwards over the expanded sacral diapophyses, and the whole propulsive effort in swimming and burrowing occurs in one plane (Palmer, 1960). Whiting (1961) extended the principle of the movable sacroiliac joint to all frogs, showing that the region undergoes lateral and vertical bendings in climbing, walking, and jumping anurans, but longitudinal slidings in aquatic and burrowing forms. He suggested that in the pipids alternating lengthening and shortening of the trunk would increase the cycle, hence the stroke, of the hindlimb thrust. He further suggested that such an adaptation, involving expanded sacral diapophyses and sliding ilia, would be advantageous for burrowing anurans either in mud bottoms or on land.

Pipids are non-jumping, powerfully swimming anurans, burrowing occasionally underwater (Dunn, 1948; Johnson, 1952), presumably utilizing the Whiting-Palmer mechanism. I suggest that Ramon and other fossil pipoids employed the same type of movement. *Thoraciliacus* achieved one extreme by its labile functional synsacrum, which drastically shortened the column to just four free segments, eliminating the lateral movements and increasing propulsion. In having four functional, free, column segments, *Thoraciliacus* is different from any living or fossil vertebrate. It displays a highly specialized aquatic adaptation, a condition that would handicap terrestrial locomotion because of inability to bend at the sacroiliac joint. This suggests that *Thoraciliacus* inhabited the more open water, whereas *Cordicephalus* may have been a marginal dweller. Also, this unique specialization may have contributed to the extinction of the thoraciliacoid line in the changing environments of the Tertiary.

Ramon frogs thus appear to have a particularly specialized pelvis, especially so in *Thoraciliacus* (Table 10). The long ilia of the anuran pelvis are a highly specialized phenomenon presumably present since the anuran grade was attained in the Triassic. The ossified pipid pubis is presumably specialized, since this element is cartilaginous in amphibamids, branchiosaurids, and *Triadobatrachus.* The alleged primitiveness of the medioiliac joint is questionable on several grounds: *Triadobatrachus* may have had anteriorly projecting ilia, though this is by no means clear. Anteriorly projecting ilia, however, are nonexistent or but little developed in Jurassic frogs; only later did this condition coexist with the normal sacroiliac joint, as evidenced by *Thoraciliacus* and *Cordicephalus* in the Cretaceous, and by paleobatrachids and xenopoids in the Tertiary. The feature is nonexistent or almost so in Recent adult pipids, discoglossids, and ascaphids. Its premetamorphic appearance in Recent unrelated frogs, as well as its prevalence among aquatic pipoids, suggest that it is paedomorphic in origin and a convergent aquatic specialization.

Limbs. The three species share most limb characters and vary but little. They agree broadly with the Recent pipid, particularly in the xenopoid manus and pes (osteological summary). All limb references, hereafter, for pipids, discoglossids, and pelobatids are to Howes and Ridewood (1888); for ascaphids to Stephenson (1952) and Ritland (1955).

Forelimb. Ramon frogs have the pipid manus pattern of four proximal carpals, inner centrale with a posterior spur, distal carpals aligned, and strikingly long metacarpals. In the latter feature they are sharply distinct from the discoglossids and ascaphids, which have short metacarpals. In carpal formula they approximate the eight of *Xenopus* rather than the six of *Pipa* or five of *Hymenochirus*, and in the diminishing order of finger length they are again like the former: 4-5-3-2. In totality, the manus is xenopoid-like with, however, an extra carpal. Ramon frogs retain the least modified anuran carpal formula, nine units including the prepollex carpal. Recent primitive anurans have eight free ossified carpals including the prepollex carpal. In adult discoglossids and pelobatids a vestige of the fifth proximal carpal appears, becoming ossified only in *Xenophrys*, the only hitherto known anuran with nine carpals. The fifth distal carpal of *Xenophrys* and of Ramon frogs corresponds to the fifth metacarpal, completing a distal carpal row of five including the prepollex.

Hindlimb. The Ramon frogs share with discoglossids and ascaphids the primitive pes condition of five distal tarsals. In this regard Ramon frogs depart from Recent pipids whose second or third distal tarsals are fused. *Cordicephalus* has an extra prehallux metatarsal which is absent in *Thoraciliacus*, but this is occasionally present along with additional phalanges in unrelated anurans, rendering it of little phylogenetic significance. The very long metatarsals and toes of Ramon frogs are as in other pipoids.

The limb similarities of Ramon frogs and *Xenopus* suggest an identity of function. The elongated fingers presumably compensate for tonguelessness in feeding, whereas the long apparently webbed toes provide powerful swimming oars. However, the pipid fore to hindlimb length ratio was significantly higher in Ramon than in Recent pipids. The ratio is 0.40 in *Hymenochirus*, 0.41 in *Xenopus*, and 0.47 in *Pipa*, whereas it is 0.56 in *Thoraciliacus*, and 0.59 in *Cordicephalus.* The higher Ramon ratio is evidently the primitive pipid condition which has decreased progressively to the low ratio of Recent pipids, which is presumably more adapted to aquatic life. Even the intergeneric difference in ratio of Ramon frogs is marginally significant (Student's $t = 2.124$; $p = 0.02–0.05$), suggesting that *Thoraciliacus* was more aquatic than *Cordicephalus*; this is in accord with the deduction from pelvic structure given above.

The presence in Ramon frogs of seven specialized and four primitive limb characters is shown in Table 10. Phylogeneti-

TABLE 8. FOSSIL RECORD OF MESOZOIC AND PALEOCENE FROGS

Period	Family	Species	Horizon and Locality	Reference
JURASSIC:				
	Notobatrachidae	*Vieraella herbstii*	L.J., Patagonia	Reig (1961)
		Notobatrachus degiustoi	M.J., Patagonia, Argentina	Reig (1957) Casamiquela (1961 b)
	Discoglossidae?	*Eodiscoglossus santonjae*	U.J., Spain	Melendez (1957) Hecht (1963)
	[1]Pipidae?	*Eobatrachus agilis*	U.J., Wyoming, U.S.A.	Hecht and Estes (1960) Hecht (1963)
	Incertae sedis	*Comobatrachus aenigmaticus*	U.J., Wyoming, U.S.A.	Hecht and Estes (1960) Hecht (1963)
	Incertae sedis	*Montsechobatrachus gaudryi*	U.J., Spain	Hecht (1963, and references).
	?	*Stremmia scaber*	U.J., Africa	Hecht (1963, and references. He denies *Stremmia*'s anuran relationships).
CRETACEOUS:				
	Pipidae	*Thoraciliacus rostriceps*	L.C., Israel	Nevo (1964 b, and present study)
	Pipidae	*Cordicephalus gracilis*	L.C., Israel	" " "
	Pipidae	*Cordicephalus longicostatus*	L.C., Israel	" " "
	Leptodactylidae	Several still undetermined forms	L.C., Texas, U.S.A.	Hecht (1963, and references).
	"Eoxenopoididae"	*Eoxenopoides reuningi*	U.C.-L.E., South Africa	Haughton (1931) Casamiquela (1961 a)
	"Eoxenopoididae"	*Saltenia ibanezi*	[2]U.C.? Argentina	Reig (1959) Casamiquela (1961 a)
	"Eoxenopoididae"	*Shelania pasquali*	U.P.-L.E., Patagonia, Argentina	Casamiquela (1961 a, 1965).
	Ascaphidae?	Unidentified genus and species	U.C., Wyoming, U.S.A.	Estes (1964)
	Discoglossidae	Cf. *Barbourula* sp.	" "	" "
	Pelobatidae?		" "	" "
	Incertae sedis, near Hylidae?		" "	" "
	Incertae sedis, near Leptodactylidae?		" "	" "
	Other anuran remains, no family assignment		" "	" "

[1] The identification of *Eobatrachus agilis* as a pipid is tentative. Hecht (1963) remarks: "If *Eobatrachus* must be assigned to any family, it is most likely closer to the Pipidae." *Eobatrachus* has been defined from a humerus.

[2] Reig (1959) described *Saltenia* as a Lower Cretaceous form. Later evidence suggests probable Upper Cretacous age (Casamiquela, personal communication).

L.J = Lower Jurassic; M.J. = Middle Jurassic; U.J. = Upper Jurassic; L.C. = Lower Cretaceous; U.C. = Upper Cretaceous; U.P.-L.E. = Upper Paleocene-Lower Eocene.

cally, the fewer the fusions the more primitive the anuran carpus and tarsus; thus the nine carpals and five distal tarsals of Ramon pipids are distinctly primitive. Conversely, the long manus and pes, and fused radioulna and tibiofibula are specialized. Noteworthily, the branchiosaurs' 2, 2, 3, 3 finger formula, and the prevalent labyrinthodont 2, 2, 3, 4, 3 toe formula are present in most anurans, probably reflecting a primitive pattern.

In summary, the limbs of Ramon frogs match the xenopoid model but are more primitive in having an extra element in both carpus and tarsus, and in their high fore- to hindlimb ratio.

Conclusions. The three Ramon species are assigned to the pipoids. They are highly variable in size, shape, and meristic characters. The first two sets of characters involve unresolved age and sex variations, the third set reflects individual variation. The types of meristic variations displayed by Ramon frogs are similar to those shown by other fossil and Recent anurans, though frequencies vary. *Thoraciliacus* is more variable than *Cordicephalus*, both in continuous and meristic variations. The highest variation in both genera is in the pelvis, the lowest in the limbs.

Ramon pipids involve a multiple-character basic adaptation to aquatic life. *Thoraciliacus* may have been more of a deep water, *Cordicephalus* more of a shallow water form. Thus, though certainly sympatric, they may have partly excluded each other competitively. Both suggest long progressive aquatic evolution of pipids. Presumably this started with emergence of the group in Triassic times and has continued ever since, at first rapidly and later at a slower rate. Aquatic adaptation was the principal factor involved in pipid origin and evolution.

Ramon pipids show a melange of 21 primitive versus 16 specialized characters. They attest to the common rule that in a given sequence no one taxon will be more primitive than others in all respects. Yet the skull, pelvis, and limbs are essentially specialized, whereas the vertebral column and pectoral girdle are mainly primitive. The two Ramon genera are the most primitive pipids yet known. *Cordicephalus* is more primitive than *Thoraciliacus.*

The Systematic Position of *Cordicephalus* and *Thoraciliacus* and Remarks on Pipoid Classification

Detailed analysis unequivocally shows the pipoid affinities of Ramon frogs but does not immediately settle their familial allocation. In fact, pipoid classification is far from settled, as is clear from recent suggested revisions of the Pipidae (Dunn, 1948; Lamotte, 1963), and pipoids (Reig, 1958; Casamiquela, 1961a) and the problematic relationships of paleobatrachids (Hecht, 1963) and rhinophrynids (Orton, 1953, 1957). Three problems are involved: (a) ranking of the lower categories within Pipidae; (b) vertical versus horizontal classification (or how to classify fossil pipoids); and (c) significance of larvae in anuran classification (or rhinophrynid relationships). The solutions to these taxonomic problems depend on evaluation of pipoid classification, the fossil record, and tadpoles.

Classification of Recent pipids. In 1830 Wagler introduced the primary divisions Aglossa and Phaneroglossa. The former has been considered taxonomically valid ever since, despite much shifting of its categorical rank (see Griffiths, 1963, for historical review). Recent studies make obsolete the African *Xenopinae* and South American *Pipinae*, recognized by Noble (1931), since the differences "cannot be considered of more than generic value" (Dunn, 1948). African *Hymenochirus* is closer to American *Pipa* than to African *Xenopus*, as evidenced by comparing the skulls (Paterson, 1945), pectoral girdles (De Villiers, 1929), and vertebral columns (Boulenger, 1899). Furthermore, Dunn regarded the three South American genera *Pipa*, *Protopipa*, and *Hemipipa* as merely three species of *Pipa*. Lamotte (1963) regards *Pseudohymenochirus* as a subgenus of *Hymenochirus*. Accordingly, the purely aquatic Recent Pipidae comprise three genera: the South American *Pipa*, with five species; African *Xenopus*, five species; and *Hymenochirus*, five species.

The Recent Pipidae, the sole family of Aglossa, are characterized by: tonguelessness, a single median opening to the eustachian tubes, azygous frontoparietals, absence of a maxillary arcade (= no quadratojugals), greatly expanded sacral diapophyses, sacrum fused to urostyle, three free

Table 9. Osteological Comparisons Among Pipoid Genera, Fossil and Recent

Character	RAMON PIPIDS		"EOXENOPOIDIDAE"			PIPIDAE			PALAEOBA-TRACHIDAE	Rank of Character
	Cordicephalus	*Thoraciliacus*	*Eoxenopoides*	*Saltenia*	*Shelania*	*Xenopus*	*Hymenochirus*	*Pipa*	*Palaeobatrachus*	
SKULL:										
Maxillary arcade incomplete	+	+	+	+	+	+	+	+	+	Superfamilial
Frontoparietals azygous	+	+	+Suture	+Suture	+Suture	+	+	+	+	Superfamilial
Maxillae and premaxillae dentigerous (D) or edentulous (E)	D	D	E	?	E	D	E	E	D	Generic
Quadratojugals absent	+	+	+	+	+	+	+	+	+	Superfamilial
Palatines absent	+	+	+	+	+	+	+	+	+	Superfamilial
Mentomandibulars absent	+	+	?	?	?	+	+	+	?	Familial?
Squamosals reduced	+	+	+	+	+	+	+	+	+	Superfamilial
Pterygoid large	+	+	+	?	?	+	+	+	+	Superfamilial
Otic capsules large	+	+	+	+	+	+	+	+	+	Superfamilial
Columella present	+	+	?	+	?	+	+	+	+	Superfamilial
Parasphenoid: sword-like (S), dagger-like (D), broad (B)	S	S	D	?	B	S	B	B	D	Generic
Nasals: broad (B), narrow (N), medium (M)	M	B	B	B?	B	N	B	B	B	Generic
Mandible edentulous	+	+	+	+	+	+	+	+	+	Superfamilial
VERTEBRAL COLUMN:										
Presacral vertebrae	8	8	6–7	8	8	8	6	7	7	Generic
Sacrum composed of the following vertebrae:	9th	9th	9th	9th	9th	9th	7th+ 8th+ 9th	8th+ 9th	7th+ 8th+ 9th	Generic
Expanded sacral diapophyses	+	+	+	+	+	+	+	+	+	Superfamilial
Postsacral vertebrae in adults	2(1)	1	0	0	0	0	0	0	0	Generic
Vertebral articulation: opisthocoely (OP), procoely (PR)	OP	OP	OP	OP	OP	OP	OP	OP	PR	Familial
Ribs in adults: free, or fused	Free	Free	Fused?	?	Free	Fused	Fused	Fused	Fused	Generic
Sacro-urostylar articulation: synostotic (S), monocondylar (M), bicondylar (B)	M	M	S	S	S	S	S	S	B	Generic
Fusion of presacrals	—	—	—	—	—	+	+	+	+	Generic
PECTORAL GIRDLE:										
Type: arciferal (A), firmisternal (F)	A	A	A	A	A	A	F	A	A	Generic
Coracoids: narrow (N), broad (B)	N	N	N	N	N	N	B	B	N	Generic

TABLE 9. *Continued*

Character	RAMON PIPIDS		"EOXENOPOIDIDAE"			PIPIDAE			PALAEOBATRACHIDAE	Rank of Character
	Cordicephalus	*Thoraciliacus*	*Eoxenopoides*	*Saltenia*	*Shelania*	*Xenopus*	*Hymenochirus*	*Pipa*	*Palaeobatrachus*	
Clavicles; arched (A), straight (S)	A	A	A	A	A	A	S	S	A	Generic
Scapula small uncleft	+	+	+	?	+	+	+	+	+	Superfamilial
Cleithrum V-shaped	+	+	+?	?	?	+	+	+	+	Superfamilial
PELVIC GIRDLE:										
Pubis ossified	+	+	+	?	?	+	+	+	+	Superfamilial
Sacroiliac articulation: medio-iliac (M), acroiliac (A)	A	M	M	M	M	A	A	A	M	Generic
LIMBS:										
Four long metacarpals	+	+	+	+	+	+	+	+	+	Superfamilial
Distal tarsals	5	5	?	?	?	4	4	4	?	Generic
Five long metatarsals	+	+	+	+	+	+	+	+	+	Superfamilial

larval ribs, basic arcifery, small uncleft scapula, large V-shaped cleithrum, and elongated metatarsals and metacarpals.

Classification of fossil pipoids. Classification of fossils always poses the alternative of horizontal versus vertical classification. The first emphasizes the uniqueness in space and time of contemporaneous related taxa; the second stresses ancestor descendant relationships of successive taxa. Should Cretaceous pipoids, the Ramon ones included, be allocated to a separate family, or assigned to Recent Pipidae?

Casamiquela (1961a), following a suggestion of Reig (1958), preferred the first alternative and established the *Eoxenopoididae*, to accommodate *Eoxenopoides*, *Shelania*, and *Saltenia* (Table 8) from the Cretaceous and Paleocene of Africa and Argentina. He brigaded *Eoxenopoididae* with *Pipidae* and *Paleobatrachidae* in the suborder Aglossa *sensu* Reig (1958) and defined the new family as having: (1) an ovoid skull; (2) a quadratojugal arch absent; (3) rhomboid frontoparietals, joined in a sagittal depression and having a longitudinal suture; (4) large otic capsules; (5) narrow styliform coracoids; (6) opisthocoelous vertebrae; (7) sacrum fused with urostyle; (8) greatly expanded sacral diapophyses, articulating with the middle portion of the ilia; and (9) hindlimb larger than forelimb.

Of those nine diagnostic characters, six are shared with Pipidae and just three (3, 4, 8) are novel. Yet all three, evaluated above, are seen to fall within individual, age, and intergeneric variations of Recent Pipidae and of *Thoraciliacus* and hence are not suitable to diagnose a new family. Even taken together they fail to show the clearly defined gap which would justify a new pipoid family. A split such as this ignores the great skeletal variation displayed by Recent pipids, which shows arcifery and firmisterny, mono- and synsacry, five to eight presacrals, and great size and shape variations. Likewise, the medioiliac joint should be considered variable in

TABLE 10. PRIMITIVE VERSUS SPECIALIZED CHARACTERS IN RAMON PIPIDS

Character	Primitive	Specialized
SKULL:		
Rostrum		+
Azygous frontoparietals		+
Large otic capsules		+
Absence of palatines, quadratojugals, and mentomandibulars		+
Reduced squamosals and maxillae		++
Dentigerous maxillae and premaxillae	+	
Plectrum of columella	+	
Ossified quadrate	+	
VERTEBRAL COLUMN:		
Eight presacral vertebrae	+	
Postsacral vertebrae	+	
Ectochordal centrum	+	
Opisthocoely	+	
No presacral fusions	+	
Free monocondylar sacro-urostylar articulation	+	
Four free ribs	+	
Monovertebral sacrum	+	
Expanded sacral diapophyses		+
Diapophyses of presacrals 6–8		+
PECTORAL GIRDLE:		
Arcifery	+	
Large clavicles	+	
Uncleft scapula	+	
Small scapula	+	
Large cleithrum	+	
No sternum, episternum, or coracoidal cartilages	+	
PELVIC GIRDLE:		
Functional synsacrum in *Thoraciliacus*		+
Ossified pubis		+
FORE LIMB:		
Developed capitate eminence		+
Developed olecranon		+
Very long metacarpals		+
Nine carpals	+	
Phalangeal formula 2, 2, 3, 3,	+	
Pointed terminal phalanges		+
HIND LIMB:		
Five distal tarsals	+	
Very long metatarsals		+
Phalangeal formula 2, 2, 3, 4, 3	+	
Pointed terminal phalanges		+

pipoids or, alternatively, *Cordicephalus* and *Thoraciliacus* should be assigned to separate families, despite all the weighty evidence that admits only a generic level of separation.

The characters distinguishing Ramon from Recent pipids, e.g. four ribs, regular presence of postsacrals, and a free sacro-urostylar joint, are certainly primitive. Yet they appear to be inappropriate as taxonomic criteria at the family level, as do eoxenopoidid characters. I suggest that eoxenopoidids and Ramon pipoids, on the contrary, be allocated to the Pipidae, which then must be slightly redefined to allow for free ribs, a sacro-urostyle joint, and postsacrals in adults. This solution would be in accord with recent lumping trends in Recent pipid classification (Dunn, 1948). Further, it will fit the general taxonomic postulate that genera tend to be horizontal, families vertical categories (Simpson, 1961). The Pipidae are a natural group embracing varied forms, but the differences between known Cretaceous and Recent pipoids cannot, I think, be considered of more than generic rank.

Other pipoids and their supposed relatives should now be briefly mentioned. The classification and relationships of the Tertiary European paleobatrachids has long been debated. They have been considered Aglossa (Špinar, 1963, and references), or as convergent to the Aglossa (Noble, 1931), or unnatural, comprising several families (Hecht, 1963). Recent studies of rich new material have led Špinar (1963) to confirm the taxonomic validity and pipoid affinities of paleobatrachids. He has revised the family, recognizing two genera and five species, and has redefined it as having seven procoelous presacrals, synsacry, five free larval ribs, fusion of presacrals 1–2, and a bicondylar sacro-urostylar joint. Pipid affinities are suggested by an incomplete maxillary arcade, azygous frontoparietals, ossified pubis, arcifery, elongated manus and pes, and five free larval ribs.

Kuhn (1941) described the genus *Opisthocoelellus* from the middle Eocene of Geiseltale, Germany, associating it with *Eoxenopoides*, and later placed it in a separate family. Hecht (1963), re-examining the material, could recognize no form ascribable to pipids.

The significance of the pipid larva, or rhinophrynid relationships.[1] Rhinophrynids have proved problematical; they were first affiliated with bufonids (Noble, 1931), later on with pipids (Orton, 1953, 1957) on the morphology of the tadpole. Griffiths (1963) has questioned the validity of basing major phylogenetic conclusions in Anura on larval characters alone. I have suggested elsewhere (Nevo, MS) that Recent pipid tadpoles are secondarily simplified, rather than primitive, basing my inferences on the sole known Cretaceous pipid tadpole (Nevo, 1956). The same suggestion, based on other grounds, was made by Tihen (1965); he, however, accepts pipid-rhinophrynid relationships on grounds of both larval and adult evidence. Adult rhinophrynids unquestionably display a mixture of primitive and specialized characters (Walker, 1938). Their primitiveness is explicit in ectochordy, large cleithrum (Meszoely, 1966), amphicoely[2] and eight carpals (personal observations). They are specialized in having a bicondylar sacro-urostyle joint, in being ribless in all stages, in their long cleft scapula, type of hyolarynx, neural arches, and limbs. Neither the primitive nor the specialized characters, it appears to me, imply pipid affinities. The former suggest ancestral proanuran, the latter terrestrial burrowing characters. Some skull characters do show similarity to pipids (Tihen, 1965; Meszoely, 1966), but others such as the complete maxillary arcade, absence of a columella, small pterygoids, and well-developed squamosals, are non-pipid. Also, postcranially, they differ from pipids in the primitive and specialized characters mentioned. All in all, I think that rhinophrynids are mosaics of primitive, basically proanuran characters, and characters specialized for burrowing, rather than pipid relatives. Both probably evolved directly from a proanuran stock into different adaptive zones, rhinophrynids into the burrowing zone, pipids into the aquatic zone.

In summary, taxonomically, pipoids comprise the Pipidae and Paleobatrachidae. The former, with a slight expansion of its definition, may appropriately accommodate both Recent and all known Cretaceous pipoids.

Pipoid Evolution

General. The evolutionary status and origin of pipids have proved problematical ever since their recognition, in contrast to their taxonomic stability. They were considered as either primitive (Noble, 1922) or specialized (Ryke, 1953, and references), and variously derived (see later). Several factors have obscured the phylogenetic status and derivation of pipids: (a) description in extreme antithetical terms as *either* primitive *or* specialized; (b) their strong and basic aquatic adaptation; (c) absence until recently of knowledge of any fossil record.

As is true of other taxa, any attempt to regard pipids as altogether primitive or specialized is doomed to failure. Pipids showed a melange of primitive and specialized characters even by early Cretaceous times (Table 10), although the specialization has, of course, increased in Recent pipids. Some of their primitive skeletal characters have long been understood as such (opisthocoely, larval ribs, large cleithra, small uncleft scapula, etc.). Conversely, long recognized specializations are the long manus and pes, loss and reduction of skull bones, vertebral fusions, etc.

---

[1] I am grateful to Mr. Charles Meszoely, who permitted me to examine the rhinophrynid skeletons he is studying.

[2] Walker (1938: 2) describes the vertebrae as opisthocoelous, but in his discussion (pp. 8–9) he compares them with ascaphid vertebrae, e.g. ectochordal and amphicoelus. Tihen (1965) regards them as opisthocoelous.

In the literature of the group, neoteny is probably the most strongly emphasized pipid characteristic. It has been considered the basic evolutionary factor in their history (De Villiers, 1934). Thus all pipid specializations have been attributed to neoteny (Millard, 1949; Ryke, 1953), which has been described as the "only common factor of this polyphyletic group" (De Villiers, 1963, personal communication). The neotenic hypothesis implies that pipids are secondarily aquatic and have regained their lateral line organs through neoteny. This hypothesis is thus not valid if pipids originated in water and have retained their primary lateral line organs (Grobbelaar, 1925). Moreover, the aquatic hypothesis stresses the *basic adaptation* involved in the origin and development of pipids rather than the specific operating *genetic mechanism.* The question, at all events, is one for which knowledge of the early environment of anurans as a whole is crucial.

Early environment and the evolutionary basis of pipids. The period of transition from proanurans to anurans is as yet undocumented by fossils. Hypotheses have been advanced for an (a) aquatic (Böker, 1935; Griffiths, 1963), (b) terrestrial (Inger, 1962), and (c) riparian (Gans and Parsons, 1966, and references) origin of frogs. The fossil evidence available suggests a probable aquatic origin. Neither *Triadobatrachus*, the probable ancestor (Griffiths, 1963), nor its Jurassic frog descendants are conceivable as terrestrials. The early true frogs, involving mainly ascaphids, discoglossids and pipids, with ecto- and stegochordy, amphi- and opisthocoely, arcifery and small scapula, present a character-complex incompatible with terrestrial life. The earliest terrestrial frogs known from the Cretaceous present holochordy, basic procoely, and long scapulae.

The concept of pre-frogs as aquatic is neither contradictory of nor incompatible with the idea of the jumping mechanism in frogs evolving while they were also using undulatory locomotion (Griffiths, 1963). Since, functionally, swimming and jumping are not incompatible (Gans and Parsons, 1966), it is conceivable that the propulsive thrust mechanism could have evolved in basically aquatic animals. It might have had the same selective advantages in water and riparian habitats, either as a means of catching food more efficiently, or of escaping from predators into mud bottoms and vegetation, or from bank into water.

The evidence of early Cretaceous pipids attests that Recent pipids have carried forward an aquatic adaptation of ancient origin, and perfection of this adaptation most probably operated as the main evolutionary selective factor since the origin of the taxon. This process has had multiple effects on the skeleton, making pipids very much water-adapted stereotypes throughout their evolution. If this thesis is true, then neither neoteny nor the potentiality of lateral line reappearance upon reinvasion of water (Escher, 1925) is necessary to account for pipid evolution.

The thesis advocating aquatic evolution of pipids stresses a *process* of progressive adaptation for the development of the taxon rather than the genetic *mechanism*(s) involved. Neoteny is neither genetically different nor more important than other ontogenetic processes involving genetic change (Simpson, 1953, and Rensch, 1960, have thoroughly evaluated the role which neoteny has played in evolution). Some probable paedomorphic characters exhibited by pipid skulls or pelves by no means violate the basis of this thesis. They presumably resulted from mutations affecting early stages of development. Other characters, including probably the majority of aquatic adaptations such as elongated manus and pes and expanded sacral diapophyses, are due to mutations affecting late ontogenetic changes.

The evolutionary interpretation of pipids is meaningful only in terms of progressive *aquatic adaptation* since their origin, probably in the Triassic. This thesis is borne out, at least inferentially, by Ramon pipids.

Phylogeny. Pipids were phylogenetically derived from: (a) discoglossids (Noble, 1925); (b) proanuran stock (De Villiers, 1929); (c) "widespread group of Anura" in late Triassic-early Jurassic times (Hecht, 1963); (d) a pipoid stem stock from which all non-ascaphid forms originated (Griffiths, 1963). Views (a), (b), and (d) are based mainly on comparative anatomy grounds, while (c) partly hinges on Orton's (1953) tadpole studies. All these views were handicapped by the scanty pipid fossil material available at the time they were proposed, yet all share the belief in *early* pipid derivation. This conception is borne out by the fossil record, which suggests to me a direct derivation of pipids from proanurans. The independent existence in the Jurassic of ascaphids, pipids, discoglossids, and possibly some representatives of the advanced frogs, favors the view of basal rapid diversification of those lines from proanurans in the Triassic; the crucial story of the transition period remains to be told.

Pipid phylogeny as conceived by this study is shown in Figure 17. The earliest known certain pipids are *Cordicephalus* and *Thoraciliacus.* Both suggest a long Jurassic evolution and probably early diversification. The cordicephaloid line, the more primitive of the two, evolved slowly into the xenopoid line in the Tertiary. The Recent genus *Xenopus*, a direct derivative of this line, is known from the Miocene of Africa (Ahl, 1926). The thoraciliacoid line, on the other hand, exhibits high aquatic specializations, particularly in the pelvis. This rapidly evolving line culminated in Cretaceous-early Tertiary times in forms like *Saltenia* and *Shelania* in South America, and *Eoxenopoides* in South Africa, thereafter becoming extinct. The paleobatrachids, apparently an independent pipoid line whose relationships and origin are still obscure, flourished for a short time in Europe during the Tertiary, becoming extinct in late Miocene times. *Pipa* and *Hymenochirus* whose direct ancestry is yet undocumented, presumably originated like *Xenopus* in the early Tertiary, while Recent species are probably late Tertiary-Pleistocene derivatives.

The overall similarities between *Cordicephalus* and Recent *Xenopus* suggest relatively slow evolutionary rates for this line during the Cenozoic. Yet structural improvements in aquatic adaptations have occurred since the Cretaceous and will be discussed below. Taxonomic diversification has presumably been limited in pipids throughout their history. Neither the three extant genera, with 15 species, nor the handful of known Cretaceous genera suggest a high level of taxonomic proliferation. However, the extinction of several pipid lines during the Tertiary may suggest somewhat higher early diversification.

Evolutionary trends. Pipids show a basic broad aquatic adaptation that has gradually improved; this is evident from comparing Ramon and Recent pipids (Table 9). The skeletal improvements involve fusions, losses, reductions, changes in ratios, increase in size, and drastic larval changes.

The vertebrae evolved from ectochordal to stegochordal, and the neural arches became imbricate. Postsacrals in adults were eliminated, and the urostyle fused to the sacrum. Fusions occurred in adults between ribs and their diapophyses, between some successive vertebrae, between carpals, and between distal tarsals. In *Pipa* and *Hymenochirus*, the number of presacrals was reduced by fusions to seven and six, respectively, and in both the teeth were lost. Skeletal ratios significantly changed; foremost among these was the change in length ratio of fore- to hindlimb from 0.59 in Cretaceous *Cordicephalus* to 0.40 in Recent *Xenopus. Hymenochirus* turned firmisternal and developed synsacry, thereby shortening its column to just five free segments. A phyletic increase in size is probable in pipids, particularly in the line leading from *Cordicephalus* to *Xenopus*, a trend indicated in many other phyletic lines by "Cope's Rule."

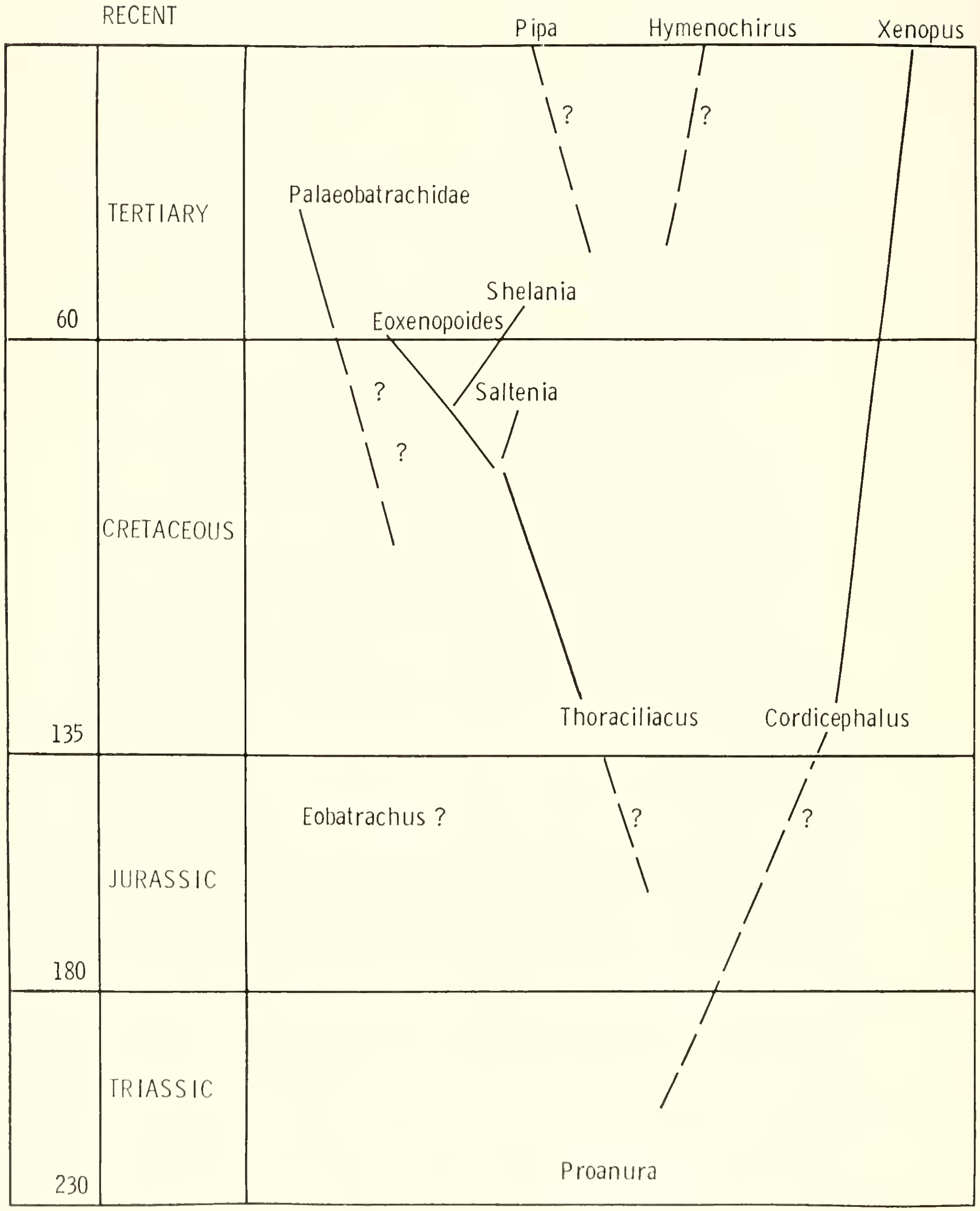


Figure 17. Diagram illustrating relationships of pipoids as suggested by this study, plotted against time scale. Continuous lines based on available fossil record; broken lines hypothetical. Left column indicates approximate time since the beginning of the periods in million of years.

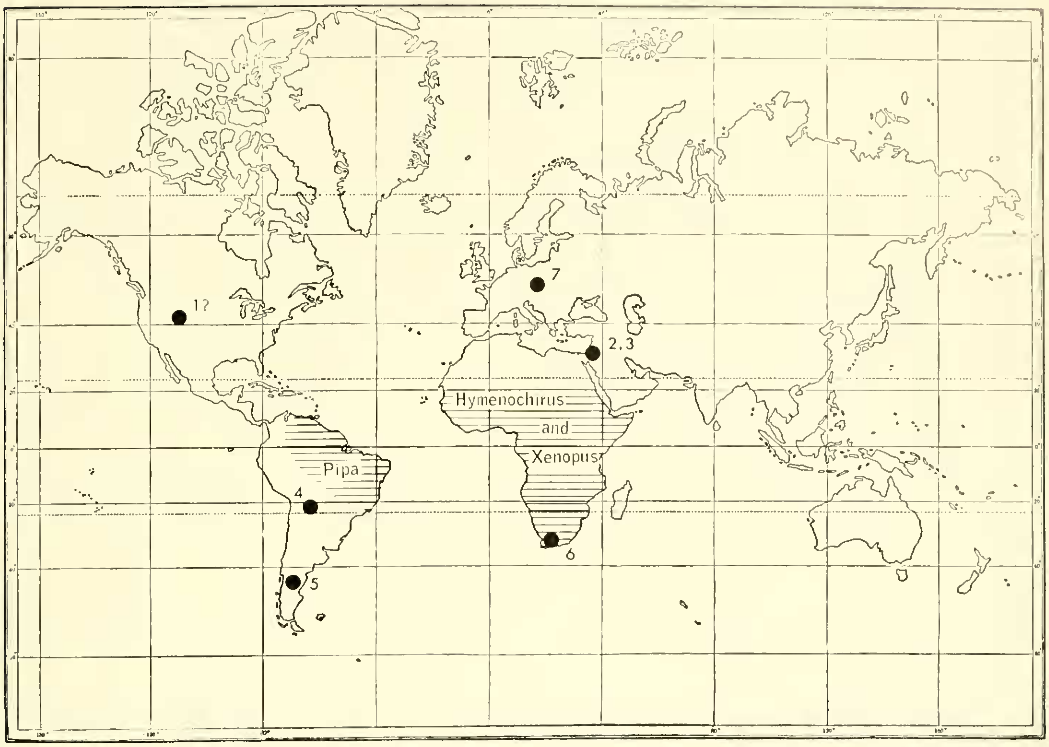


Figure 18. The distribution of Recent and fossil pipoids. Recent pipids are indicated by horizontal lines: in South America—*Pipa*; in Africa—*Xenopus* and *Hymenachirus*. Fossil pipoids are indicated by numbered circles: 1. *Eobatrachus agilis*; 2, 3, *Thoraciliacus* and *Cardicephalus*; 4. *Saltenia ibanezi*; 5. *Shelania pasquali* 6. *Eoxenopoides reuningi* and *Xenopus strameri*; 7. *Palaeobatrachidae*.

The most impressive modification pipids underwent is in the evolution of their larvae. Their ancestral larva had tail vertebrae (Nevo, 1956) as in the Recent *Megophrys major* (Griffiths, 1956). Paleobatrachids had normal tadpoles without caudal vertebrae in the Miocene. If this reflects the condition of the contemporaneous pipid larva in the Tertiary, then the change from the ancestral to the present secondarily simplified larva occurred in late Cretaceous-early Tertiary times.

Paleogeography. The distribution of Recent and fossil pipoids is shown in Figure 18. At present, pipids have a disjunct distribution, mostly in the tropics of the old and new worlds. This pattern is a remnant of a pipid distribution over the greater part of the world during Cretaceous times, possibly extending back into the Jurassic, as suggested by the fossil record. The ever changing, often contradictory views on anuran centers of origin and dispersal routes testify to the near impossibility of a sound zoogeography unless documented by fossils. Furthermore, even the fossil record, which is rare and accidental in frogs, particularly in terrestrial ones, may be misleading unless it is documented by evidence of early radiations. In frogs such radiations presumably occurred in the Triassic, and are as yet undocumented.

The history of fossil pipoid discoveries illustrates perfectly how postulates of place and time of origin are directly related to successive fossil finds. The rich paleobatrachid finds early in the last century, from the Tertiary of Europe, added support to the Holarctic school advocating a northern origin of Anura (Noble, 1931). The Cretaceous *Eoxenopoides* from South Africa supported the postulate, based mainly on the distribution of modern forms, that the Old World tropics was the sought-for center (Darlington, 1957). The subsequent discoveries of *Saltenia* and *Shelania* from the Cretaceous and Paleocene of Argentina, plus the Jurassic *Notobatrachus*, suggested South America as the pipoid center of origin (Casamiquela, 1961a). Similar logic might now suggest Asia as the pipid center, based on Ramon pipids. Evidently, however, the crucial discoveries which will elucidate centers of origin of pipids and other early frog lineages are yet to be made in continental Triassic rocks.

SUMMARY AND CONCLUSIONS

1. The fossil record of frogs is more complete than has been realized, particularly for pipids, and must be considered in evolutionary interpretations along with studies of Recent forms.
2. The Ramon frog collection permits studies of the whole skeleton of great numbers. Consequently, it enables population studies of inter- and intraspecific variations, population dynamics, adaptive complex, and phylogenetic interpretation.
3. All Cretaceous pipoids may be referred to Recent Pipidae.
4. The evidence of Ramon and other Cretaceous pipids suggests that:
   - (a) Pipids have been an independent aquatic line, at least since the Jurassic, and they probably were derived directly from proanurans in Triassic times.
   - (b) Pipids are primarily aquatic; their origin and evolution involve a basic aquatic adaptive complex progressively improving in aquatic co-adaptation.
   - (c) Pipids are, and have always been, a melange of ancestral and specialized characters, yet the latter proportionately increase in time. The skull, pelvis, and limbs specialized early in pipid evolution, whereas the column and pectoral girdle always lagged behind.
   - (d) Evolutionary trends in the pipid skeleton involve structural changes, fusions, losses, reductions, ratio changes, and increase in size. Most are explicable as improvements in aquatic adaptation.
   - (e) Pipids have probably never been taxonomically prolific, yet their record suggests a rapid basal limited diversification, then some Tertiary extinctions, and later a slower generic and specific splitting in the Tertiary.
   - (f) The cordicephalid line appears to be ancestral to the xenopid; the thoraciliacid line is related to "eoxenopoidids," but became extinct in Tertiary times.
   - (g) Pipids had an almost worldwide distribution in the Cretaceous and probably in late Jurassic times; their center of origin is as yet unknown.

REFERENCES CITED

AHL, E. 1926. Anura; Aglossa, Xenopodidae. *In*: Kaiser, Erich, Die Diamantenwüste Südwest-Afrikas. Berlin, D. Reimer, Vol. 2, pp. 141–142.

BENTOR, Y. K. AND A. VROMAN. 1951. The geological map of the Negev, 1:100.000, sheet 18: Abde (Ovdat), 1st ed., 98 pp. [In Hebrew.]

BÖKER, H. 1935. Einführung in die vergleichende biologische Anatomie der Wirbeltiere. Jena, Gustav Fischer, Vol. 1, xi + 228 pp.

BOULENGER, G. A. 1899. On *Hymenochirus*, a new type of aglossal batrachians. Ann. Mag. Nat. Hist., (7) 4: 122–125.

CASAMIQUELA, R. M. 1961a. Un pipoideo fósil de Patagonia. Rev. Mus. La Plata, Sec. Paleont., N.S. 4: 71–123.

———. 1961b. Nuevos materiales de *Notobatrachus deginstoi* Reig. La significación del anuro Jurásico Patagónico. Rev. Mus. La Plata, Sec. Paleont., N.S. 4: 35–69.

———. 1965. Nuevos ejemplares de *Shelania pascuali* (Anura, Pipoidea) del Eoterciario de la Patagonia. Ameghiniana, **4** (2): 41–51.

———. 1966. Nuevo material de *Vieraella herbstii* Reig. Reinterpretación de la ranita liásica de la Patagonia y consideraciones sobre filogenia y systemática de los anuros. Rev. Mus. La Plata, Sec. Paleont., N.S. **4**: 265–317.

Colbert, E. H. 1964. Climatic zonation and terrestrial faunas. *In*: Nairn, A. E. M. (ed.), Problems in Paleoclimatology. New York, John Wiley and Sons, pp. 617–637.

Darlington, P. J. 1957. Zoogeography: The Geographical Distribution of Animals. New York, John Wiley and Sons, xiii + 675 pp.

De Villiers, C. G. S. 1924. On the anatomy of the breast-shoulder apparatus of *Xenopus*. Ann. Transvaal Mus., **10** (4): 197–211.

———. 1929. The comparative anatomy of the breast-shoulder apparatus of the three aglossal anuran genera: *Xenopus, Pipa*, and *Hymenochirus*. Ann. Transvaal Mus., **13**: 37–69.

———. 1934. Some points in the anatomy of *Microbatrachella capensis* Hewitt, and their bearing upon the question of phylogenetic neoteny. S. Afr. J. Sci., **31**: 406–414.

Dunn, E. R. 1948. American frogs of the family Pipidae. Amer. Mus. Novit., No. **1384**: 1–13.

Eaton, T. H. 1959. The ancestry of modern Amphibia: A review of the evidence. Univ. Kansas Publ. Mus. Nat. Hist., **12** (2): 155–180.

Eiselt, J. 1941. Der Musculus opercularis und die mittlere Ohrsphäre der Anuren Amphibien. Arch. Naturg., (N.F.) **10** (2): 179–230.

Escher, K. 1925. Das Verhalten der Seitenorgane der Wirbeltiere und ihrer Nerven beim Übergang zum Landleben. Acta. Zool. (Stockholm), **6**: 307–414.

Estes, R. 1964. Fossil vertebrates from the late Cretaceous Lance Formation, eastern Wyoming. Univ. Calif. Publ. Geol. Sci., **49**: 1–187.

———. 1965. Fossil salamanders and salamander origins. Amer. Zool., **5**: 319–334.

Gadow, H. 1933. The Evolution of the Vertebral Column. London, Cambridge Univ. Press, 356 pp.

Gans, C. and T. S. Parsons. 1966. On the origin of the jumping mechanism in frogs. Evolution, **20**: 92–99.

Green, T. L. 1931. On the pelvis of the Anura: A study in adaptation and recapitulation. Proc. Zool. Soc. London, **1931**, pt. 4: 1259–1291.

Griffiths, I. 1956. The status of *Protobatrachus massinoti*. Nature (London), **177**: 342–343.

———. 1963. The phylogeny of the Salientia. Biol. Rev., **38**: 241–292.

Grobbelaar, C. S. 1925. Beiträge zu einer anatomischen Monographie von *Xenopus laevis* (Daud.). Z. Anat. Entwickl. Ges., **72**: 131–168.

Guardabassi, A. 1955. Su alcune anomalie dello scheletro assile di *Xenopus laevis*. Arch. Zool. Ital., **40**: 321–346.

Haughton, S. H. 1931. On a collection of fossil frogs from the clays at Banke. Trans. Roy. Soc. S. Africa, **19**: 223–249.

Hecht, M. K. 1962. A reevaluation of the early history of the frogs. Part I. Syst. Zool., **11**: 39–44.

———. 1963. A reevaluation of the early history of the frogs. Part II. Syst. Zool., **12** (1): 20–35.

Hecht, M. K. and R. Estes. 1960. Fossil amphibians from Quarry Nine. Postilla, Yale Peabody Mus. Nat. Hist., **46**: 1–19.

Hodler, F. 1949. Untersuchungen über die Entwicklung von Sacralwirbel und Urostyl bei den Anuren. Ein Beitrag zur Deutung des anuren Amphibientypus. Rev. Suisse Zool., **56** (39): 747–790.

Howes, G. B. and W. Ridewood. 1888. On the carpus and tarsus of the Anura. Proc. Zool. Soc. London, **1888**: 141–182.

Hsiao, S. D. 1934. A comparative study of the pectoral region of some typical Chinese Salientia. Peking Nat. Hist. Bull., **8**: 169–204.

Inger, R. F. 1962. On the terrestrial origin of frogs. Copeia, **1962**, No. 4: 835–836.

Israel Geological Society Makhtesh Ramon Symposium. 1963. Israel Geol. Soc., pp. 1–20.

Johnson, M. L. 1952. Herpetological notes from northeastern Brazil. Copeia, **1952**, No. 4: 283–284.

Kuhn, O. 1941. Die eozänen Anura aus dem Geiseltale. Nova Acta Leopoldina, (N. F.) **10** (71): 345–376.

———. 1962. Die vorzeitlichen Frösche und Salamander, ihre Gattungen und Familien. Jh. Ver. Vaterl. Naturk. Württemberg, **117**: 327–372.

Lamotte, M. 1963. Contribution à l'étude des batraciens de l'Ouest Africain. XVII. Le développement larvaire de *Hymenochirus* (*Pseudohymenochirus*) *merlini* Chabanaud. Bull. I. F. A. N., **25**, sér. A (3): 944–953.

Lorch, J. 1963. The fossil flora of Makhtesh Ramon. *In*: Israel Geol. Soc. Makh. Ram. Symp., 1963: 15.

Lowenstam, H. A. 1964. Paleotemperatures of the Permian and Cretaceous periods. *In*: Nairn, A. E. M. (ed.), Problems in Paleoclimatology. New York, John Wiley and Sons, pp. 227–248.

Melendez, Bermudo. 1957. Leonardi's "La Evolucion Biologica." Ediciones Fax, 450 pp.

Meszoely, C. A. M. 1966. Osteology of the burrowing toad *Rhinophrynus dorsalis.* Abst. 46th Ann. Meeting Amer. Soc. Ich. Herp., Miami, Florida, June 1966.

Millard, N. 1949. The development of the venous system of *Xenopus laevis.* Trans. Roy. Soc. S. Africa, **32** (1): 55–99.

Mookerjee, H. K. 1931. On the development of the vertebral column of Anura. Phil. Trans. Roy. Soc. London, Ser. B., **219:** 165–195.

Nevo, E. 1955. The Jurassic of Makhtesh Ramon. Geol. Surv. Israel, Jerusalem, unpublished report, 25 pp.

———. 1956. Fossil frogs from a Lower Cretaceous bed in southern Israel (central Negev). Nature (London), **178:** 1191–1192.

———. 1963. The Jurassic strata of Makhtesh Ramon. Israel J. Earth Sci., **12** (2): 90–91.

———. 1964a. Fossil urodeles in early Lower Cretaceous deposits of Makhtesh Ramon, Israel. Nature (London), **201** (4917): 415–416.

———. 1964b. Population studies of anurans from the Lower Cretaceous of Makhtesh Ramon, Israel. Doctoral Dissertation, Hebrew Univ., Jerusalem, iv + 128 pp.

Noble, G. K. 1922. The phylogeny of the Salientia. I. The osteology and the thigh musculature; their bearing on classification and phylogeny. Bull. Amer. Mus. Nat. Hist., **46:** 1–87.

———. 1925. The evolution and dispersal of the frogs. Amer. Nat., **59:** 265–271.

———. 1931. The Biology of the Amphibia. New York, McGraw Hill Book Co., 577 pp.

Orton, G. L. 1953. The systematics of vertebrate larvae. Syst. Zool., **2:** 63–75.

———. 1957. Larval evolution and frog classification. Syst. Zool., **6:** 79–86.

Palmer, M. 1960. Expanded ilio-sacral joint in the toad *Xenopus laevis.* Nature (London), **187** (4739): 797–798.

Parsons, T. S. and E. E. Williams. 1963. The relationships of the modern Amphibia: A reexamination. Quart. Rev. Biol., **38** (1): 26–53.

Paterson, N. F. 1939. The head of *Xenopus laevis.* Quart. J. Micr. Sci., **81:** 161–234.

———. 1945. The skull of *Hymenochirus curtipes.* Proc. Zool. Soc. London, **115:** 327–354.

———. 1955. The skull of the toad *Hemipipa carvalhoi* Mir. Rib. with remarks on other Pipidae. Proc. Zool. Soc. London, **125:** 223–252.

———. 1960. The inner ear of some members of the Pipidae (Amphibia). Proc. Zool. Soc. London, **134** (4): 509–546.

Piveteau, J. 1937. Un amphibien du Trias inférieur. Essai sur l'origine et l'évolution des amphibien anoures. Ann. Paléont., **26:** 135–177.

Proctor, J. B. 1921. On the variation of the scapula in the batrachian groups Aglossa and Arcifera. Proc. Zool. Soc. London, **1921:** 197–214.

Ramaswami, L. S. 1939. Some aspects of the anatomy of Anura (Amphibia). A review. Proc. Indian Acad. Sci., **10:** 41–80.

Reig, O. A. 1957. Los anuros del Matildense. *In:* Stipanicic, P. N. and O. A. Reig, El "Complejo Porfírico de la Patagonia Extraandina" y su fauna de anuros. Acta Geol. Lilloana, **1:** 231–297.

———. 1958. Proposiciones para una nueva macrosistemática de los anuros. (Nota preliminar.) Physis, **21:** 109–118.

———. 1959. Primeros datos descriptivos sobre los anuros del Eocretáceo de la provincia de Salta (Rep. Argentina). Ameghiniana, **1** (4): 3–8.

———. 1961. Noticia sobre un nuevo anuro fósil del Jurásico de Santa Cruz (Patagonia). Ameghiniana, **2** (5): 73–78.

———. 1964. El problema del origen monofilético o polifilético de los anfibios, con consideraciones sobre las relaciones entre anuros, urodelos y ápodos. Ameghiniana, **3:** 191–211.

Rensch, B. 1960. Evolution Above the Species Level. New York, Columbia Univ. Press, 419 pp.

Ritland, R. M. 1955. Studies on the post-cranial morphology of *Ascaphus truei.* I. Skeleton and spinal nerves. J. Morphol., **97** (1): 119–178.

Ryke, P. A. J. 1953. The ontogenetic development of the somatic musculature of the trunk of the aglossal anuran *Xenopus laevis* (Daudin). Acta Zool. (Stockholm), **34** (1): 1–70.

Sanders, O. 1953. A rapid method for preparing skeletons from preserved Salientia. Herpetologica, **9** (1): 48.

Schaeffer, B. 1949. Anurans from the early Tertiary of Patagonia. Bull. Amer. Mus. Nat. Hist., **93** (2): 41–68.

Sedra, S. N. and M. I. Michael. 1957. The development of the skull, visceral arches, larynx and visceral muscles of the South African clawed toad *Xenopus laevis* (Daudin) during the process of metamorphosis (from stage 55 to stage 66). Verh. Nederlandse Akad. Wet. Naturk., **51:** 1–80.

Shilo, A. and E. Nevo. 1955. [The Lower Cretaceous of Makhtesh Ramon.] Geol. Surv. Israel, Jerusalem, unpublished report, 6 pp. [In Hebrew.]

Simpson, G. G. 1953. The Major Features of Evolution. New York, Columbia Univ. Press, 434 pp.

———. 1961. Principles of Animal Taxonomy. New York, Columbia Univ. Press, 247 pp.

Smit, A. L. 1953. The ontogenesis of the vertebral column of *Xenopus laevis* (Daudin) with special reference to the segmentation of the metotic region of the skull. Ann. Univ. Stellenbosch, **29** A (3): 79–136.

Špinar, Z. 1963. Der vorläufige Bericht über einige Ergebnisse des Studiums von Fröschen der Familie Paleobatrachidae Cope, 1889. Věst. Ústr. Úst. Geol., **38**: 201–204.

Stephenson, E. M. 1952. The vertebral column and appendicular skeleton of *Leiopelma hochstetteri* (Fitzinger). Trans. Roy. Soc. New Zealand, **79** (3–4): 601–613.

Teixeira, C. 1948. Flora Mesozoica Portuguesa. Geol. Surv. Portugal, Lisbon, 119 pp.

Tihen, J. A. 1965. Evolutionary trends in frogs. Amer. Zool., **5**: 309–318.

Van Bergeijk, W. A. 1959. Hydrostatic balancing mechanism of *Xenopus laevis* larvae. J. Acous. Soc. Amer., **31**: 1340–1347.

———. 1967. The evolution of vertebrate hearing. *In*: Neff, W. D. (ed.), Contributions to Sensory Physiology, Vol. II: 1–44. New York, Academic Press.

Vose, G. P. 1958. A water immersion technique for producing high detail radiographs of laboratory animals. J. Biol. Phot. Assoc., **26** (2): 81–86.

Walker, C. F. 1938. The structure and systematic relationships of the genus *Rhinophrynus*. Occ. Pap. Mus. Zool. Univ. Michigan, **372**: 1–11.

Whiting, H. P. 1961. Pelvic girdle in amphibian locomotion. *In*: Vertebrate Locomotion. Zool. Soc. London Symposium, **5**: 43–57.

Williams, T. W. 1941. Alizarine red S and toluidine blue for differentiating adult or embryonic bone and cartilage. Stain Technology, **16** (1): 23–25.

Witschi, E., J. A. Bruner, and W. A. Van Bergeijk. 1953. The ear of the adult *Xenopus*. Anat. Rec., **117** (Abstr. 161): 602–603.

Woods, H. 1912. A monograph of the Cretaceous Lamellibranchia of England. London, Palaeontogr. Soc., 2 vols.

(Received 15 December 1966.)

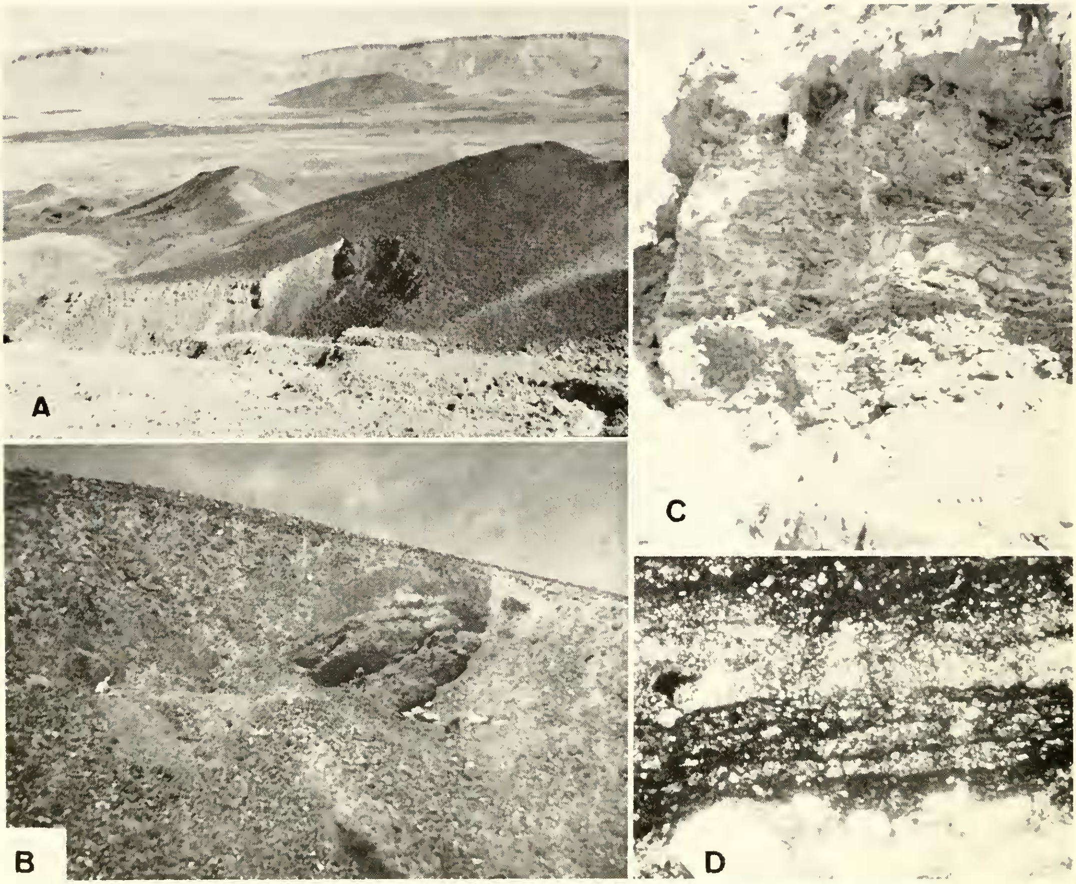


Plate 1. The Amphibian Hill locality in western Makhtesh Ramon, Israel.

A. Regional view of western Makhtesh Ramon. The rim is made up of Cenomanian formations, overlying the Nubian Sandstone which forms the slope. The black hills are composed of the upper and lower basalts of early Cretaceous age. The black basalt hill in the right half of the photograph is the Amphibian Hill comprising the exposure from which all the frog collection has been dug. This exposure is progressively enlarged by increasing closeups in Figures B, C, and D.

B. The silt unit comprising the frogs is seen as a tilted lens overlying the lower basalt and underlying the upper basalt. The lens tapers out under the basalt cover.

C. A closeup of the amphibian bed, showing the laminated deposit.

D. A thin section of the rock comprising the frog bed, magnified × 30. Note the white laminations consisting of quartz grains and alternating with the black hematitic-limonitic laminae which contain the fossil frogs.

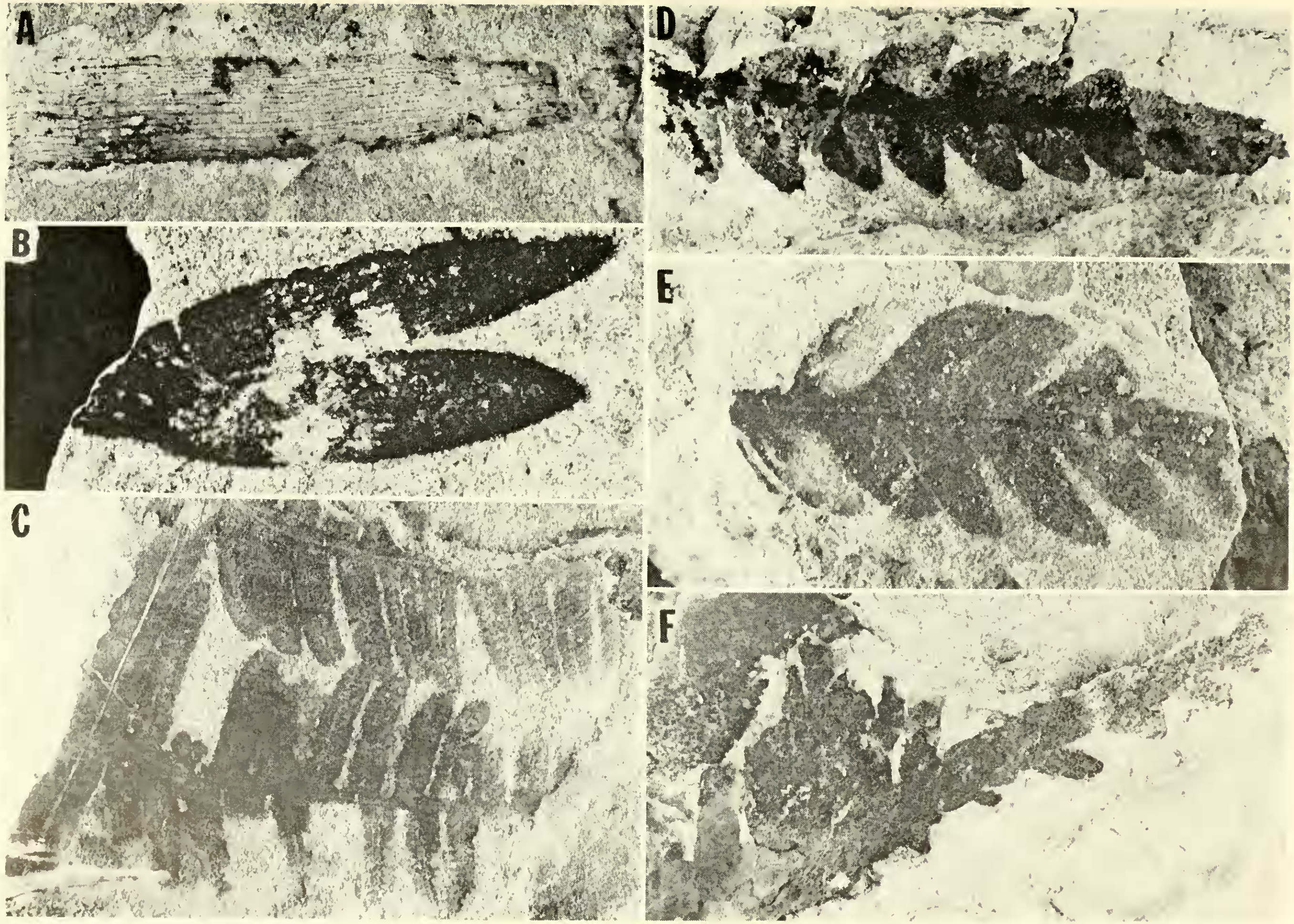


Plate 2. Lower Cretaceous fossil plants from the amphibian bed, Makhtesh Ramon. A. *Podozamites* sp.; B. *Schizolepis* sp.; C. *Phlebopteris fertile* ?; D. *Cladophlebis* sp. E. *Cladophlebis* sp.; F. *Brachyphyllum obesum*. (Identification of plants was kindly provided by Dr. J. Lorch, Department of Botany, Hebrew University, Jerusalem.)

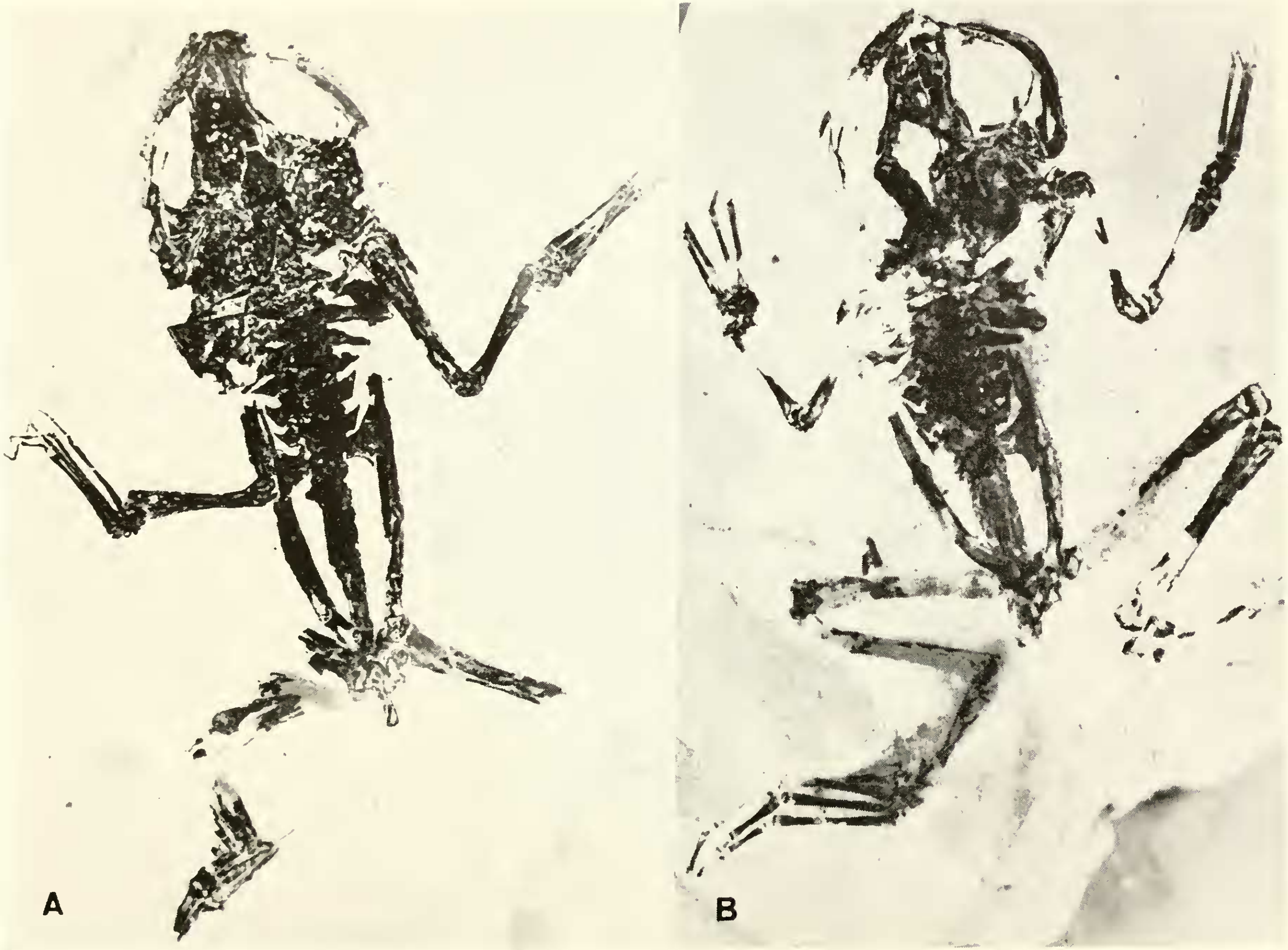


Plate 3. *Thoraciliacus rostriceps* n.g., n. sp., early Cretaceous, Makhtesh Ramon, Israel. All specimens of the species were collected from the same deposit, shown on Plate 1, fig. C, magnified × 3. All are deposited in the Hebrew University, Jerusalem, Department of Zoology, abbreviated to HUJZ. A. Type specimen, HUJZ, F 93; compare with drawing of Figure 4. B. HUJZ, F 85; an almost complete specimen showing most of the species characteristics.

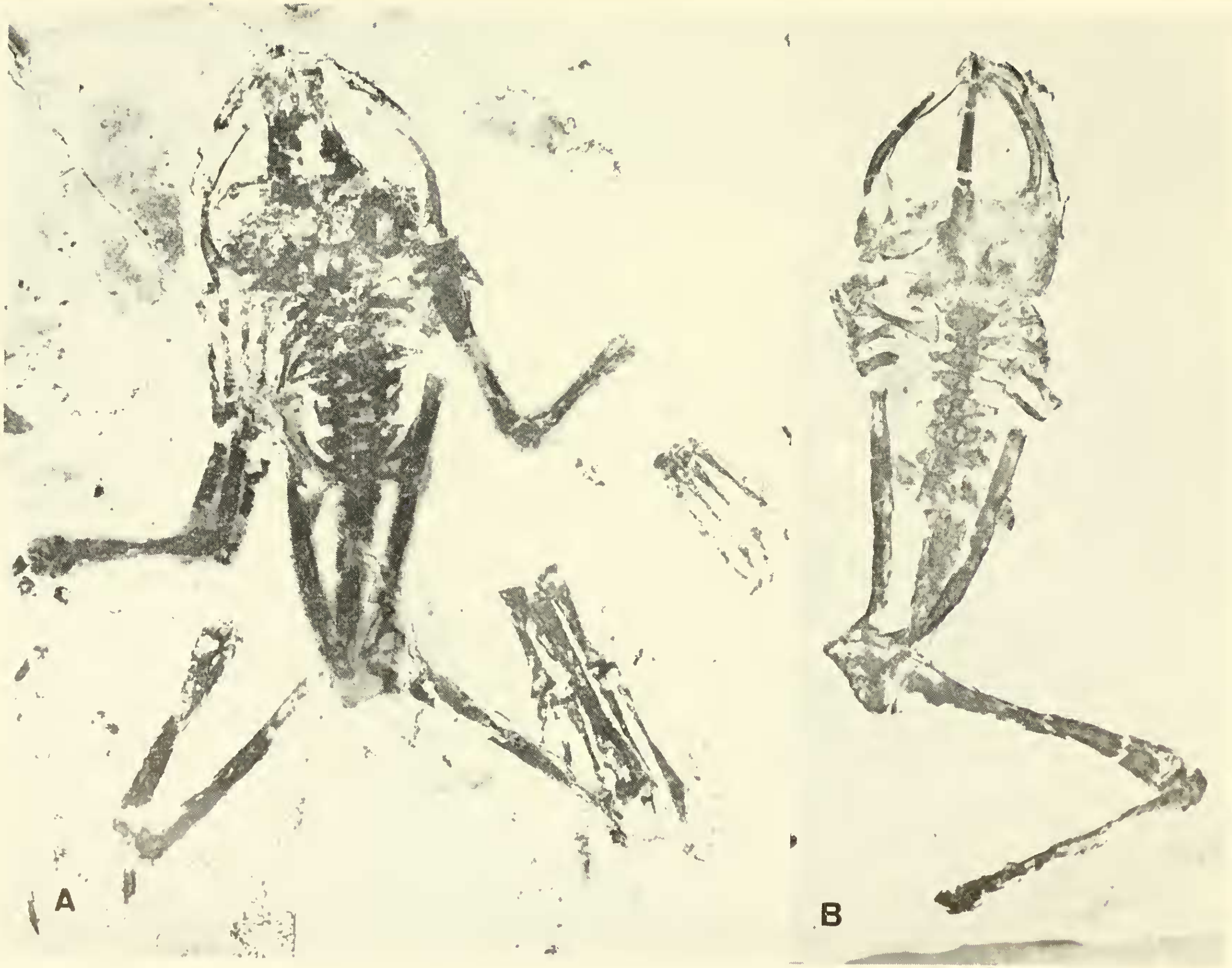


Plate 4. *Tharaciliocus rostriceps*, magnified × 3. A. HUJZ, F 70 b. Note details of skull, scapula, ribs, anterior ilia and postsacral vertebra. B. HUJZ, F 40. Note dentigerous premaxillae and maxillae, parasphenoid, coracoid, four free ribs, postsacral vertebra, and hour-glass effect in presacrals.

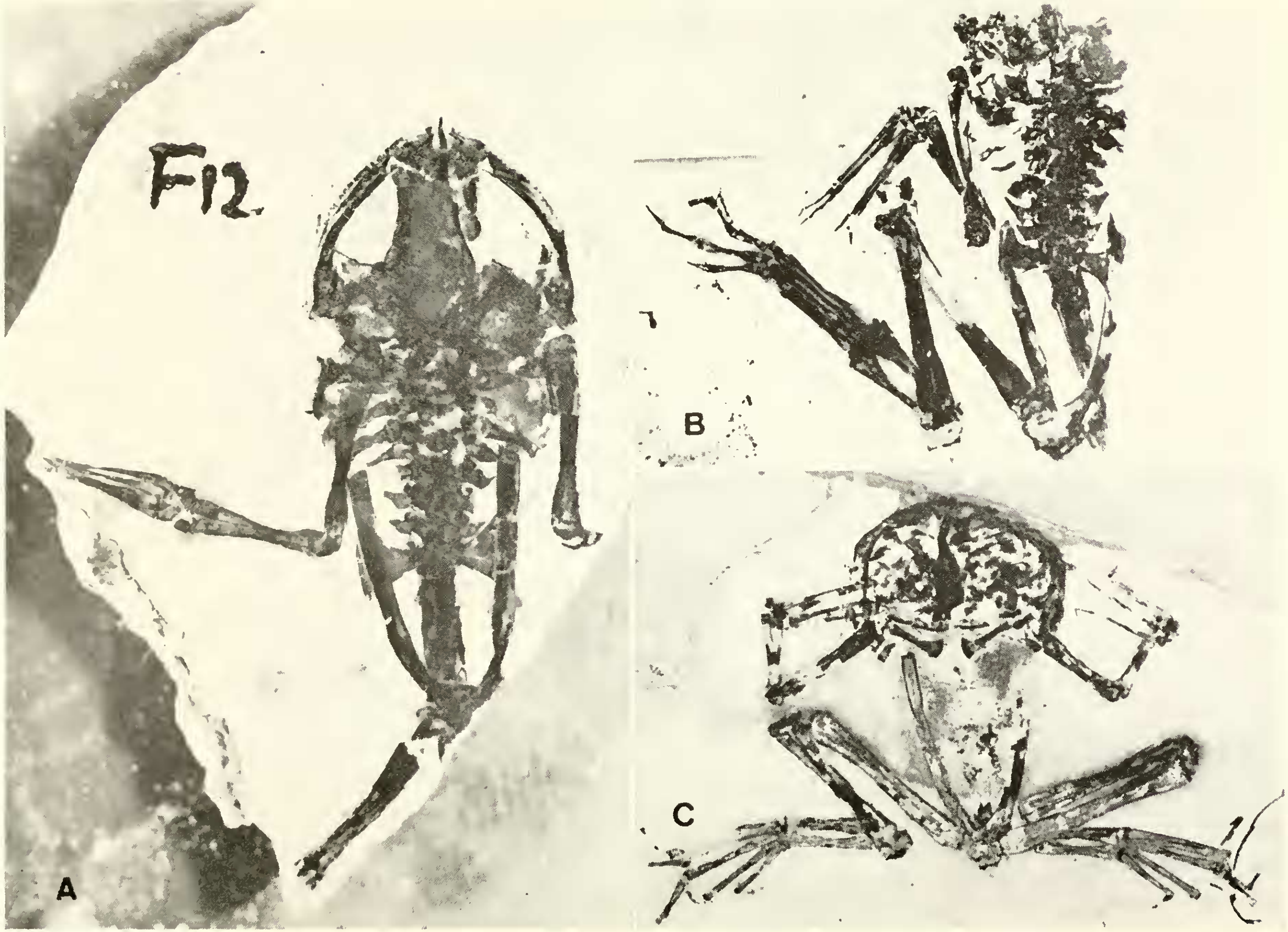


Plate 5. *Tharaciliacus rastriceps.* A. HUJZ, F 12; note azygous frontoparietals, incomplete dentigerous maxillary arcade, extensive otic capsules, four ribs, medioiliac articulation, carpals. B. HUJZ, F 110 b; note elongated manus and pes. C. HUJZ, F 124; note complete pectoral girdle and anteriorly extended ilia.

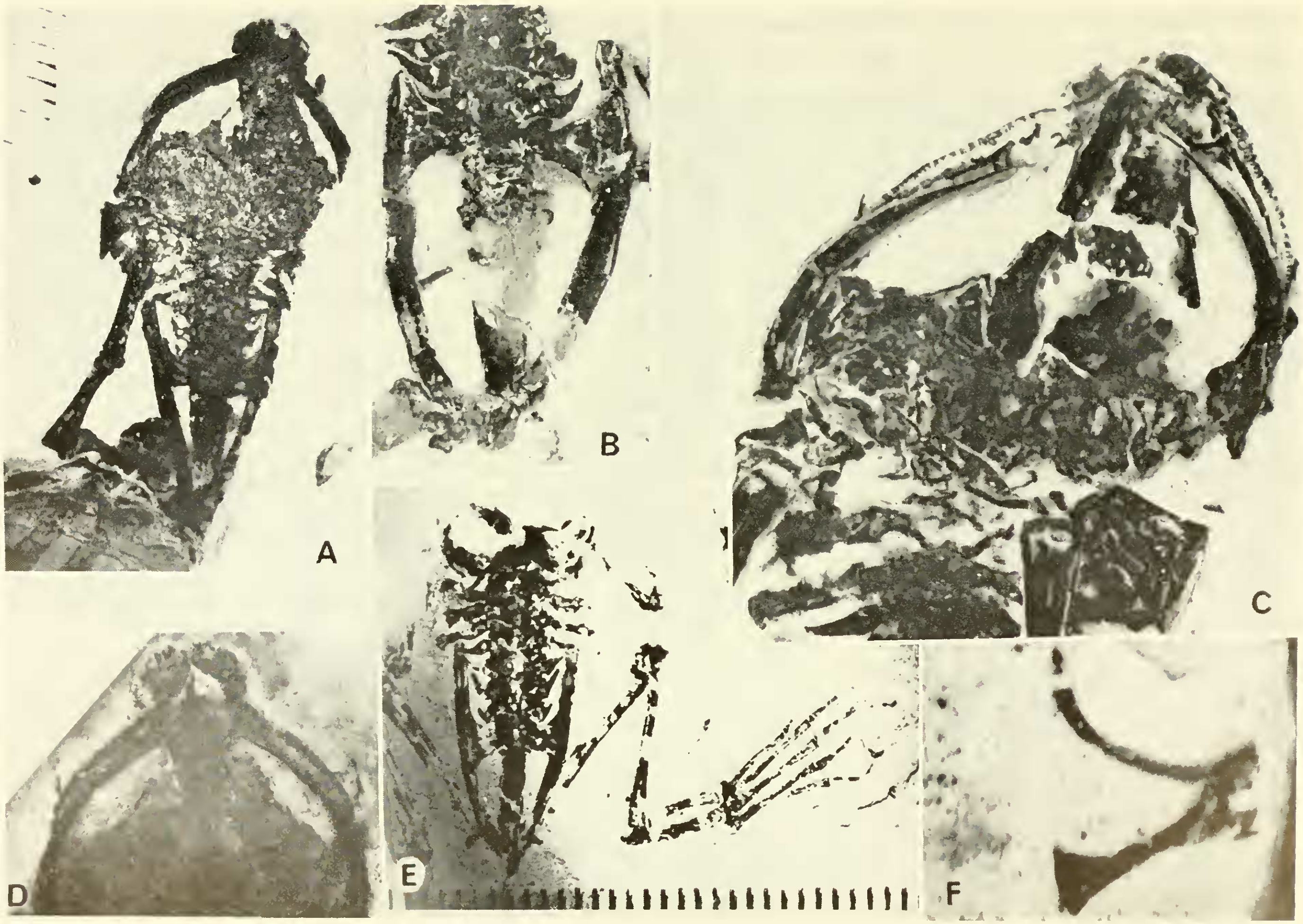


Plate 6. *Thoraciliacus rostriceps*, magnified × 3 unless otherwise specified. A. HUJZ, F 1 a; note rostrum, uncleft scapula, ribs, medioiliac articulation. The ilia contact the appendages of presacrals 4, 5, and 9. B. HUJZ, F 112; note three postsacrals. C. HUJZ, F 20, × 6; note teeth, parasphenoid, pectoral girdle. D. HUJZ, F 53; skull magnified × 6; note the rostrum consisting of the two nasals. E. HUJZ, F 41 a; note four ribs, medioiliac articulation, long pes. F. HUJZ, F 237; coracoid and clavicle, magnified × 6, in natural position.

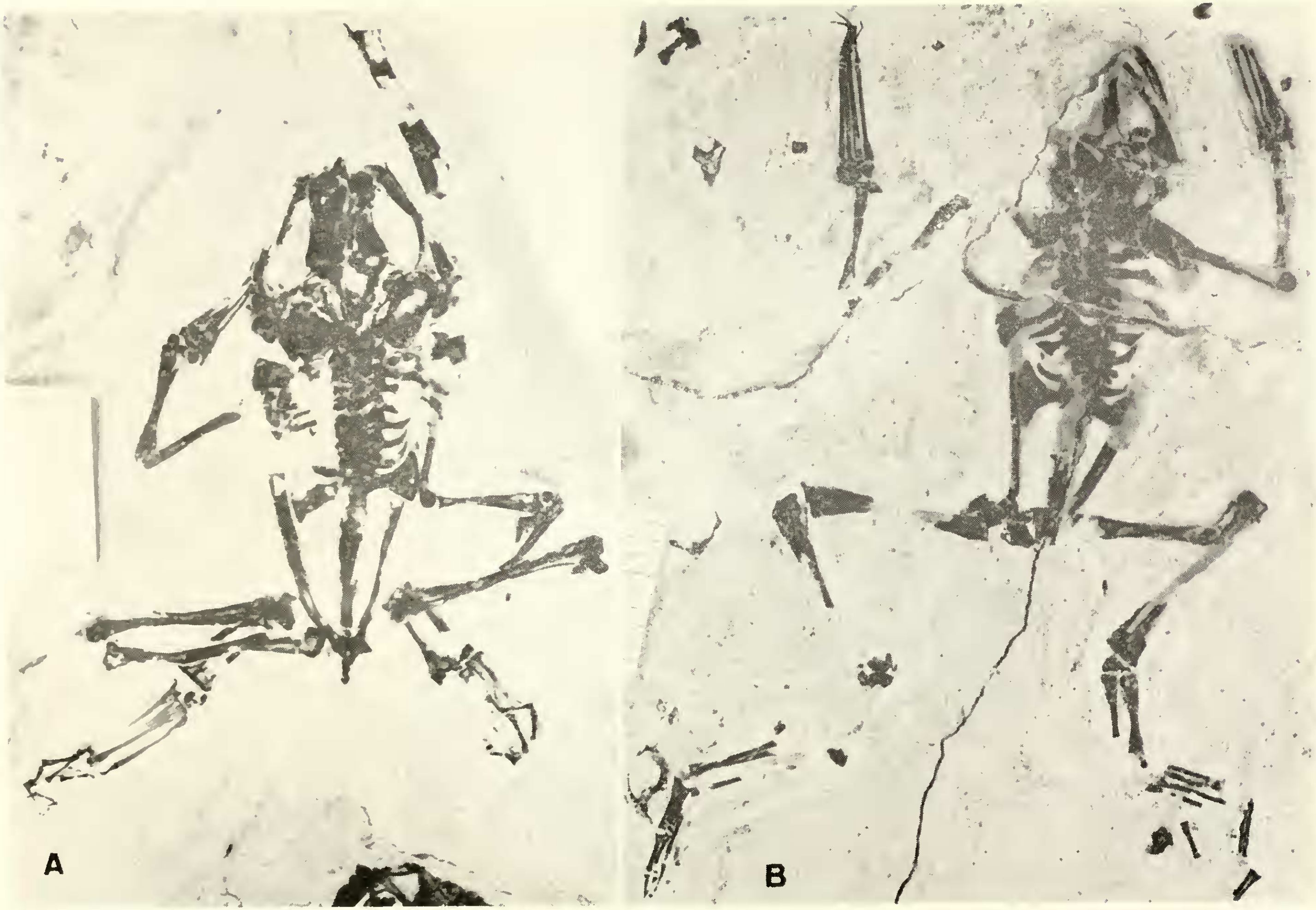


Plate 7. *Cardicephalus gracilis* n. gen., n. sp., early Cretaceous western Makhtesh Ramon, Israel; magnified × 3. A. Type specimen, HUJZ, F 165 a; compare drawing of Figure 6. B. HUJZ, F 168 a; note manus, pes, long ribs, and acroiliac articulation.

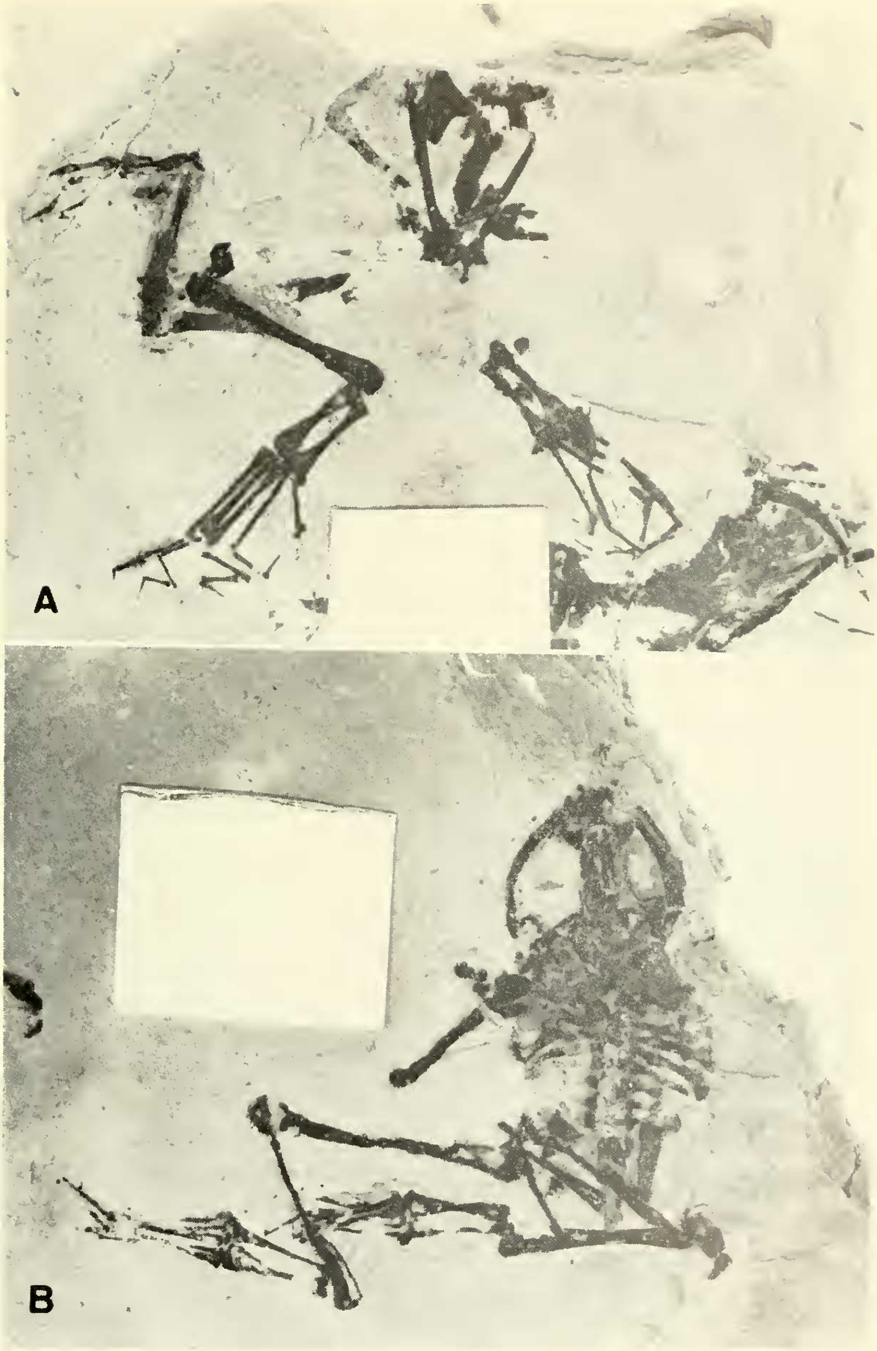


Plate 8. *Cordicephalus gracilis*, magnified × 3. A. HUJZ, F 177; note triangular pelvis, shape of sacral diapophysis, elongated pes with terminal pointed phalanges. B. HUJZ, F 197; note skull and four long ribs.

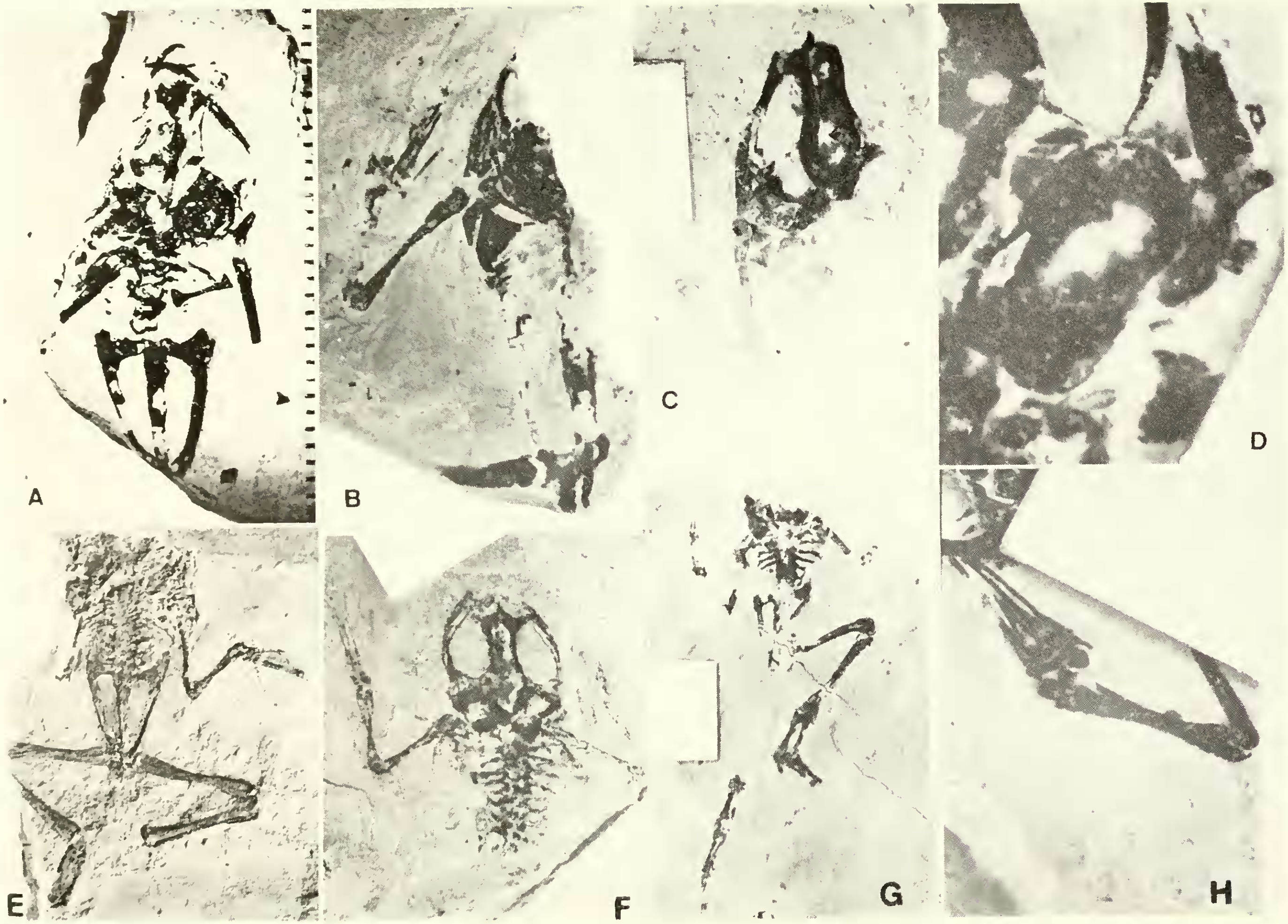


Plate 9. *Cordicepholus gracilis*, magnified × 3 unless otherwise specified. A. HUJZ, F 176 a; note coracoid and acroiliac articulation. B. HUJZ, F 201; note columella, coracoid, scapula, suprascapula and cleithrum. C. HUJZ, F 179 a; note shape of frontoparietals. D. HUJZ, F 165 a; note otic capsule, columella and operculum; × 9.5. E. HUJZ, F 151 b; × 2.2; note slenderness of the skeleton, long ribs, acroiliac articulation, triangular shape of pelvis. F. HUJZ, F 170 a; × 2; note skull and slenderness of skeleton. G. HUJZ, F 158; × 2; note ribs. H. HUJZ, F 165 a; × 6; note the shape and number of carpals; compare with Figure 6.

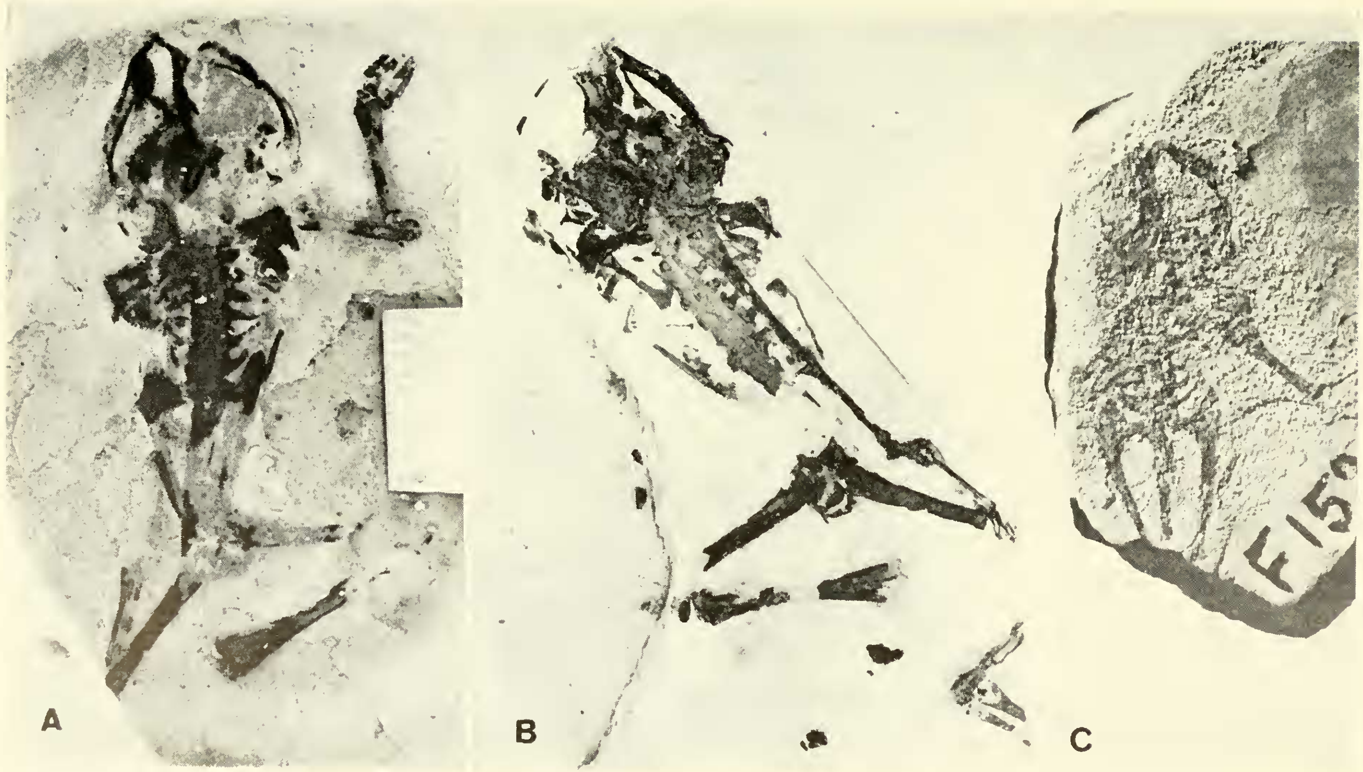


Plate 10. *Cardicephalus longicastatus* n. sp., early Cretaceous western Makhtesh Ramon, Israel. A. Type specimen, HUJZ F 171 a; compare with drawing on Figure 8. B. Counterpart of type specimen, HUJZ, F 171 b. C. HUJZ, F 152 a; note type of pelvis and the diapophyses of presacrals 6–8.

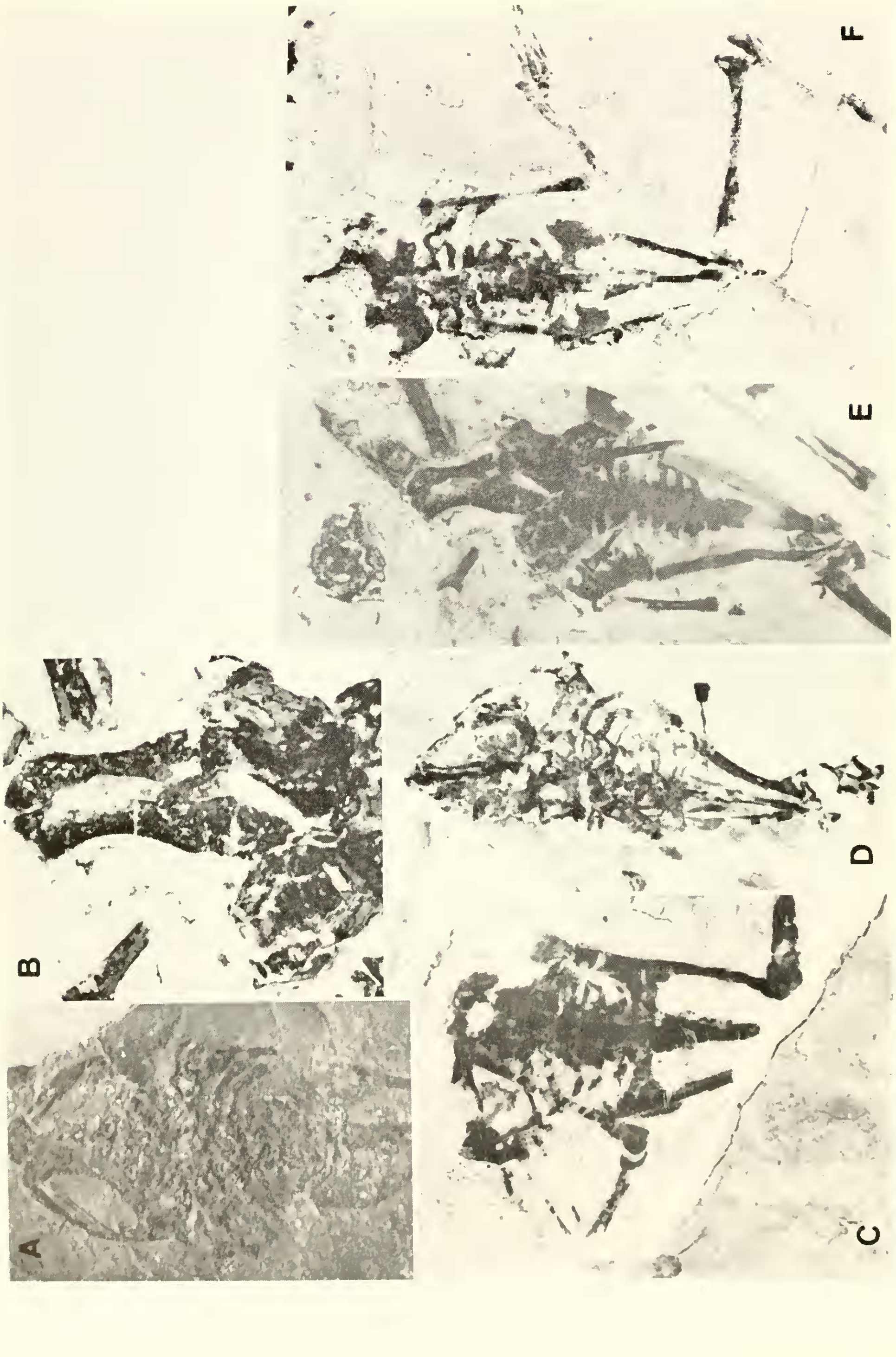


Plate 11. *Cardicephalus longicostatus*, magnified × 3. A. HUJZ, F 150 a; note four very long ribs. B. HUJZ, F 188; skull magnified × 6; note frontoparietals, subquadrangular shape of otic capsule, and bent columella on left side of the left otic capsule. C. HUJZ, F 185; note long humerus, capitate eminence, olecranon and elongated, manus. D. HUJZ, F 189 a; note long ribs and separated ischiopubic complex. E. HUJZ, F 188; note skull (enlarged on Fig. B on this plate), coracoid, and cleft scapula. F. HUJZ, F 156; note long ribs and long humerus, acroiliac articulation, and shape of pelvis.